

Skull of *Catopithecus browni*, an Early Tertiary Catarrhine

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ABSTRACT Fossil crania from quarry L-41, Fayum, Egypt, representing *Catopithecus browni*, a primate similar in size to callitrichids but with a catarrhine dental formula, provide the geologically earliest record of an anthropoidean skull. *Catopithecus* had postorbital closure developed to the stage seen in extant anthropoideans, with direct contact between zygomatic plate and maxillary tuber, isolating an anterior orbital fissure from the inferior orbital fissure. The auditory region also resembles that of later anthropoideans: The posterior carotid foramen is placed adjacent to the jugular fossa; a large promontory canal crosses the promontorium; and the annular ectotympanic is fused ventrally to the bulla. The incisors and canines show an assemblage of features found only among modern anthropoideans and adapoids. The face is characterized by a relatively deep maxilla, broad ascending wing of the premaxilla, and long nasal bones, yielding a moderate muzzle similar to that of *Aegyptopithecus*. The small braincase bears an anteriorly broad frontal trigon and a posteriorly developed sagittal crest. The mandibular symphysis is unfused even in mature adults. The encephalization quotient (EQ) probably falls within the range of Eocene prosimians, much lower than the EQs of Neogene anthropoideans. © 1996 Wiley-Liss, Inc.

Catopithecus browni is a fossil anthropoidean primate found in early Tertiary sediments of the Fayum Depression, Egypt (Simons, 1989, 1990). The cranial description presented here is based on material collected during the field seasons of 1988 to 1994 at quarry L-41, the geologically oldest of the Fayum sites that has yielded fossil primates, and one of the oldest primate sites in Africa (Bown and Kraus, 1988; Rasmussen et al., 1992; Godinot, 1994; Simons and Rasmussen, 1995). *Catopithecus* is the most ancient anthropoidean primate represented by cranial remains. Six cranial specimens from quarry L-41 are nearly complete, but each one is crushed. Consequently, the amount of anatomical detail that can be discerned on any one specimen is limited. With the recovery of several specimens, each

yielding a few unique morphological details, it has become possible to compile a thorough craniology of *Catopithecus*.

The skull of *Catopithecus* is of importance in addressing many questions in primate evolution. In particular, the skull of this early anthropoidean is central to phylogenetic inquiry about the origin of Anthropoidea, to questions about the adaptations of the earliest anthropoideans, and to questions about the evolution of individual morphological characters among anthropoidean and catarrhine primates. The purpose of this report is to make the craniology of *Cato-*

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pithecus available to researchers interested in these and other related questions. The first part of the article presents a brief historical overview of the study of early anthropoid crania, followed by morphological descriptions and comparisons of the skull of *Catopithecus*. Finally, we conclude with a discussion of the implications of the cranium of *Catopithecus* to anthropoid phylogeny, adaptation, and character evolution.

The skull of *Catopithecus* has been discussed briefly in a few previous publications (Simons, 1990, 1995a,b, Simons and Rasmussen, 1995). In this contribution, we review the larger sample of fossils now available and present detailed new observations about 1) the construction of the postorbital septum; 2) orbital orientation and proportions; 3) morphology of the cranial vault and estimates of brain size; 4) anatomy of the basicranium including a few details about middle ear structure.

HISTORY OF STUDY

Early anthropoid crania

The first discoveries of fossil anthropoid crania of any great antiquity were specimens of South American monkeys (Bluntschli, 1931; Rusconi, 1933, 1935; Kraglievich, 1951; Hershkovitz, 1970, 1974). The early South American finds, now attributed to the genera *Homunculus* (Bluntschli, 1931), *Tremacebus* (Rusconi, 1933, 1935), and *Dolichocebus* (Kraglievich, 1951), were considered to be Oligocene in age at the time of their discovery; all are now viewed as no older than early Miocene (MacFadden et al., 1985; MacFadden, 1990; Hartwig, 1994). Hershkovitz (1974) interpreted the one known cranium of *Tremacebus* as having primitively incomplete postorbital closure; later investigators have shown that the apparently open socket in that specimen is a consequence of breakage (Rose and Fleagle, 1981; Fleagle and Rosenberger, 1983). These fossil platyrrhine skulls are now viewed as having essentially modern morphology.

Prior to the discovery of these New World crania, the earliest reasonably complete skull of an Old World fossil anthropoid was of *Mesopithecus*, a Pliocene genus then known from Pikermi, Greece (Gaudry, 1862).

The first discovery of a catarrhine skull as old as the early Miocene was that of *Proconsul* found by Mary Leakey in 1948 on Rusinga Island, Kenya (Clark and Leakey, 1951; Walker et al., 1983). The skull is roughly the same age as the oldest platyrrhine crania (early Miocene; Pickford, 1981). For about a decade following its discovery, this skull of *Proconsul* and a fragmentary lower face and posterior braincase of a juvenile found at Rusinga in 1951 (Davis and Napier, 1963) served as the only examples of early catarrhine cranial morphology.

From the late 1950s through the 1960s, several other crania were found of Miocene and much older Oligocene anthropoids. The wave of new finds was led by the discovery of a beautifully preserved skull of *Pliopithecus vindobonensis* (Zapfe, 1958, 1960), which exhibited some primitive features by catarrhine standards (e.g., absence of a tubular ectotympanic). This discovery was followed by the finding of a crushed skeleton and skull of *Oreopithecus bambolii* in late Miocene deposits of Italy (Hürzeler, 1960; Straus and Schön, 1960).

At about the same time, a bone fragment in the American Museum of Natural History collected in the Fayum, Egypt in 1908 was recognized as the frontal bone of a probable parapithecoid primate (Simons, 1959, 1995a,b), a group of Oligocene anthropoids known at the time by two partial lower jaws (Osborn, 1908; Schlosser, 1911; Kälin, 1961). The primate status of the parapithecoids had been questioned (Hürzeler, 1956; Piveteau, 1957), and the metopic fusion and postorbital closure evident in the frontal bone specimen were to become pivotal in demonstrating that parapithecoids were anthropoid primates. This frontal bone, now known to be attributable to *Apidium phiomense* (Simons, 1995a), helped stimulate Simons' interest in the Fayum, leading him to initiate a long series of Fayum expeditions spanning the time from 1961 to the present.

All direct knowledge of Paleogene anthropoid crania comes from the Jebel Qatrani Formation of the Fayum Depression, Egypt. The general history of fieldwork in the Fayum is presented elsewhere (Simons, 1968; Simons et al., 1978; Simons and Ras-

mussen, 1990; Gingerich, 1992). During the first series of trips to Egypt (the Yale-Cairo expeditions, 1961–1967), additional skull fragments of *Apidium phiomense* were found to supplement the American Museum frontal bone, including pieces of the maxilla, frontal, and temporal bones and nearly complete mandibles. Subsequent analyses of these specimens appeared in several publications (Gingerich, 1973; Simons and Delson, 1978; Cartmill et al., 1981; Fleagle and Rosenberger, 1983). These fossils plus additional cranial remains of parapithecids found during the second series of Fayum field projects (the Duke-Cairo expeditions, 1977 to the present) have continued to play a central role in understanding the early anthropoidean cranium (Fleagle and Kay, 1987). Recent Fayum expeditions have unearthed even more complete cranial specimens of both *Apidium* and *Parapithecus* (Simons, 1995a).

Meanwhile, another Fayum primate, *Aegyptopithecus*, became the focus of attention for craniological studies of early anthropoideans through the recovery of a nearly complete skull on Fayum quarry M during the 1966 field season. The specimen was missing only parts of the cranial vault and basicranium, and the four incisors (Simons, 1967, 1972; Radinsky, 1973). Over the course of a few years in the 1960s, *Aegyptopithecus* had risen from its status as one of the most obscure of the Fayum genera to become the best known catarrhine of the early Tertiary. Additional cranial finds of *Aegyptopithecus* were made during the Duke-Cairo expeditions. Well-preserved faces were found in 1981, 1982, 1986, and 1988. A female cranium was found in 1985, and a second male cranium was recovered in 1986 (Simons, 1982, 1987, 1993; Simons and Rasmussen, 1989; Leakey et al., 1991). With increasing interest in the origin of Anthropoidea, cranial features of *Aegyptopithecus* became a central focus of research (Cachel, 1975, 1979a; Kay and Simons, 1980; Fleagle and Rosenberger, 1983; Fleagle and Kay, 1985; Harrison, 1987; Simons and Rasmussen, 1989; Leakey et al., 1991; Benefit and McCrossin, 1993).

During the same time interval when these Fayum discoveries were being made, addi-

tional catarrhine crania were also found in African sites of early to middle Miocene age (Fleagle and Simons, 1978; Leakey et al., 1988a,b; Teaford et al., 1988; Benefit and McCrossin, 1989, 1993). Nine catarrhine genera dated between about 15 and 35 million years of age are now known by substantial cranial material (*Apidium*, *Parapithecus*, *Aegyptopithecus*, *Pliopithecus*, *Afropithecus*, *Turkanapithecus*, *Proconsul*, *Micropithecus*, *Victoriapithecus*.) All these Oligocene and Miocene finds have now been exceeded in age and in number of nearly complete cranial specimens by *Catopithecus browni*.

Catopithecus

Quarry L-41 is an unusual site that has become the most productive mammal locality in the Fayum region (Bown and Kraus, 1988; Rasmussen and Simons, 1991). It is also the oldest Fayum site that has yielded fossil primates, probably being late Eocene in age (Simons, 1989; Van Couvering and Harris, 1991; Kappelman et al., 1992; Rasmussen et al., 1992; Simons and Rasmussen, 1995; but see Gingerich, 1992, 1993, who interpreted the age as early Oligocene). The first identifiable primates were recovered from the quarry in 1988 (Simons and Rasmussen, 1995). Cranial remains from this site are typically flattened to various degrees. Despite the crushing, many specimens are unusually complete, implying minimal disturbance between death and burial in sediment. The crushing is primarily diagenetic. Many of the fossils are poorly mineralized and extremely delicate, requiring immediate application of hardeners before careful removal from the quarry. The matrix is a fine-grained mudstone with an unusual, salty chemical composition containing about 12% sodium chloride. The specimens are extremely hydrophilic as a consequence of their salinity, and if they are allowed to absorb atmospheric moisture they disintegrate. The salt content causes permanent problems for long-term conservation and molding of specimens. The depositional environment and taphonomic conditions that led to the accumulation of thousands of dead animals with only moderate postmortem deterioration of bone in a few meters thickness

of fine-grained mud remain mysterious. Taphonomic studies are in progress.

Catopithecus browni was described as a new genus and species based on upper and lower partial dentitions from quarry L-41 (Simons, 1989). The new form was shown to be related to the larger species *Oligopithecus savagei*, known only by dental specimens from younger quarry E (Simons, 1962; Rasmussen and Simons, 1988). The taxonomic description was followed by an account of the first fossil skull (Fig. 1; Simons, 1990), which confirmed the anthropoid status of *Catopithecus* by virtue of its postorbital closure. This was important because the cheek teeth of *Catopithecus*, like those of *Oligopithecus*, are similar to those of Eocene adapoids in many respects; long ago, *Oligopithecus* had been classified as adapoid by some researchers (Szalay, 1970; Gingerich, 1977). Additional description, comparison, and analysis of the first skull of *Catopithecus* appeared subsequently (Rasmussen and Simons, 1992; Simons et al., 1994), along with a report on a few, fragmented postcrania possibly referable to the genus (Gebo et al., 1994). In the meantime, more skulls were retrieved from quarry L-41, with the laborious preparation of the delicate specimens being undertaken at the Duke University Primate Center. A second cranium has been illustrated previously (Fig. 1; Simons and Rasmussen, 1995). Third and fourth crania provided additional data used in a brief report on the anterior dentition and other diagnostic anthropoid features (Figs. 2, 3; Simons, 1995b). Complete anatomical detail from these specimens and from additional crania and isolated skull fragments found during recent field seasons are published here for the first time.

FOSSIL MATERIAL

Summary data on the six primary crania of *Catopithecus* are presented in Table 1. Additional specimens of fragmentary crania, mandibles, and teeth are mentioned in the text by accession number. Institutional abbreviations are as follows: AMNH, American Museum of Natural History, New York; CGM, Cairo Geological Museum, Cairo; DPC, Duke University Primate Center, Dur-

ham, North Carolina; YPM, Yale Peabody Museum, New Haven, Connecticut.

ANATOMY

Facial skeleton

Orbital region. *Catopithecus* had postorbital closure developed to the stage seen in extant anthropoids. This was first documented by cranium 1 (Simons, 1990). The right side of cranium 1 shows a broken and displaced zygomatic portion of the postorbital plate and partial exposure of the frontal contribution to the plate. The badly crushed left side can be interpreted as showing a broad postorbital plate continuous with the lateral braincase wall of the temporal fossa; unfortunately, this side is poorly preserved and the interpretation is ambiguous. Neither side provides good views of the shape and position of the inferior orbital fissure, nor of the postorbital portion of the alisphenoid bone (Simons, 1990).

Crania 2, 3, and 5 are relatively well preserved in the right postorbital region. In cranium 2, the postorbital region has been plastically deformed by dorsoventral crushing, but the region is basically intact. In cranium 3, the frontal component of the right orbit has been crushed downward into the lower part of the orbit, thereby detaching it from its suture with the zygomatic bone. The cup-shaped postorbital plate of the zygomatic bone has retained its shape with minimal bending (Fig. 2). In cranium 5, the inferior portion of the postorbital septum is fragmented, but the superior portion of the zygomatic bone does fuse with the lateral braincase.

The zygomatic bone of cranium 3 extends backward and downward in a broad, curved plate behind the eye. The lower edge of the zygomatic portion of the postorbital plate is of particular interest; there is evidence of zygomatic-maxillary fusion across the inferior orbital fissure, dividing the fissure into small anterolateral and larger posteromedial portions. A continuous, unbroken bone surface therefore connects the cupped zygomatic postorbital plate with the maxillary tuber (Fig. 4). The anterolateral part of the fissure that has been pinched off from the main fissure has been named the anterior

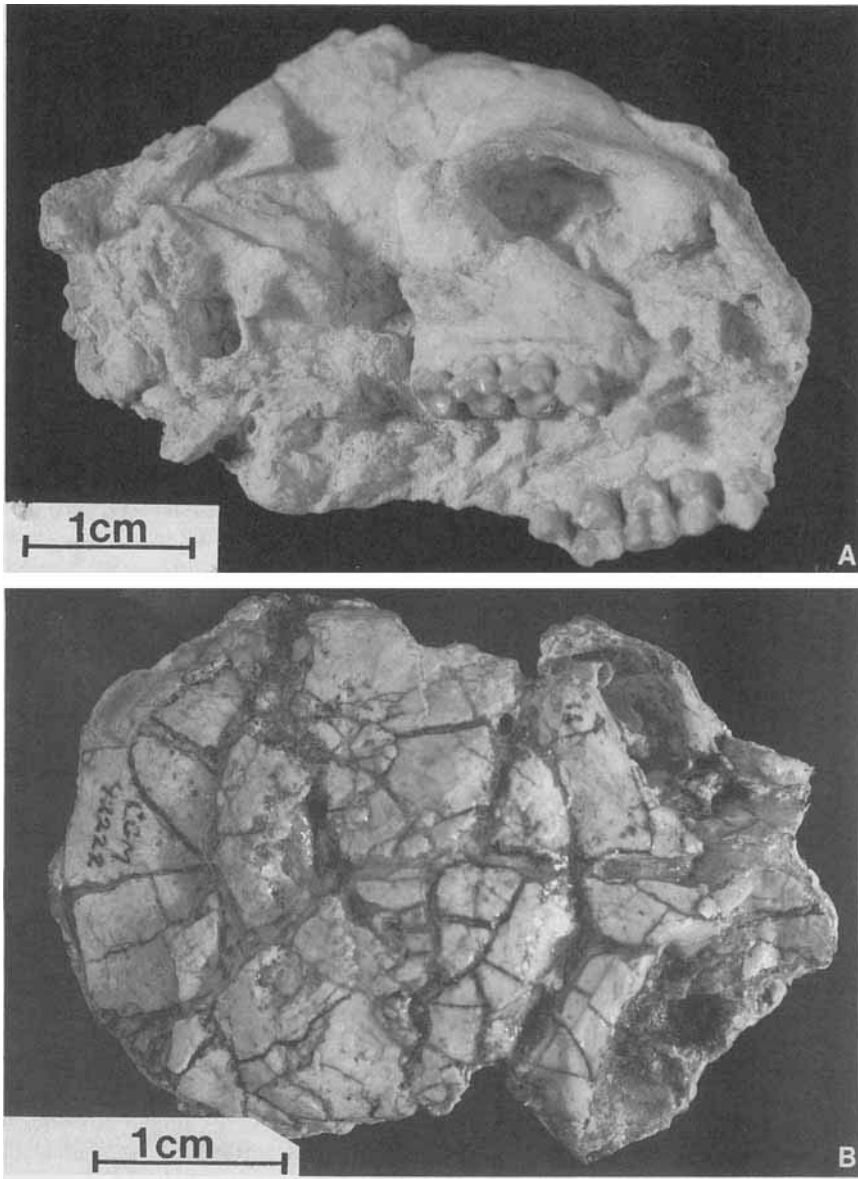


Fig. 1. Photographs of two crania of *Catopithecus browni*. **A:** Cranium 1 (DPC 8701), which is crushed near the sagittal plane, showing the right orbit, right and left cheek teeth, right external acoustic meatus, nuchal cresting, and occipital condyles. **B:** Cranium 2 (CGM 42222) in dorsal view showing the broad interorbital region, the somewhat divergent orbits, and the oval crushed braincase.

orbital fissure (Cartmill, 1980). The shape of this opening is lenticular in cranium 3. The small anterior orbital fissure variably present in *Callithrix* is typically rounder; the broader homologous opening in *Aotus* (which is confluent with the inferior orbital fissure

proper) is broader than in *Catopithecus* and lenticular in shape. Medial to the zygomatic-maxillary bone bridge of cranium 3, the main part of the inferior orbital fissure cannot be traced because of crushing. In cranium 2, however, the main inferior orbital fissure is

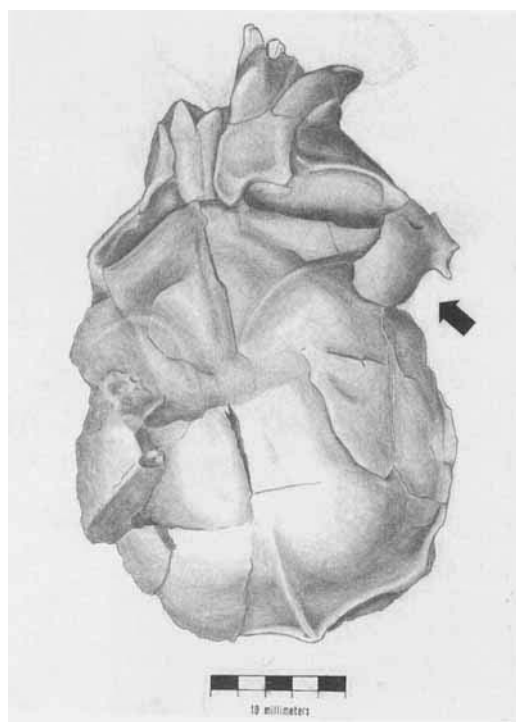


Fig. 2. Dorsal view of cranium 3 (DPC 11388). Note the presence of two right fragmentary incisors; the large ascending wing of the premaxilla; the long, pointed nasal bones; the right postorbital plate of the zygomatic bone (the black arrow indicates the angle of view used to prepare Fig. 4); the posterior sagittal crest and pronounced external occipital protuberance.

better preserved, and shows a moderate slit-like opening of a size falling within the range of modern anthropoids.

An anterior orbital fissure occurs variably in some extant genera (e.g., *Callithrix*, *Saimiri*), while in other taxa the anterior orbital fissure is usually sealed shut (Hershkovitz, 1974; Cartmill, 1980). In some taxa, the inferior orbital fissure is relatively open throughout its length to the base of the zygomatic arch (subsuming the anterior orbital fissure), either as a thin slit or as a relatively broad opening (e.g., *Aotus*). The relative size, breadth and anatomical relationships of the lateral part of the postorbital plate of *Catopithecus* fall within the range of variation of modern anthropoids.

A partial cranium of another L-41 primate, *Proteopithecus sylviae* (Simons, 1989), exhibits a well-preserved postorbital plate.

Its inferior orbital fissure is comparable to that of *Aotus*, having a mediolaterally wide inferior orbital fissure, and a notable constriction in the middle where the zygomatic dips toward the maxillary tuber, but does not contact it. At least one specimen of *Aegyptopithecus zeuxis* (DPC 8794) has the lateral part of the inferior orbital fissure closed, without an anterior orbital fissure. Taken together, these three Fayum taxa show variation from a broadly open inferior orbital fissure (*P. sylviae*), to a bridged zygomatic-maxillary contact sequestering an anterior orbital fissure (*C. browni*), to a reduced fissure that is laterally sutured shut (*A. zeuxis*). This is not an evolutionary sequence because all three conditions persist in various anthropoids today.

Although crania 2 and 3 preserve the inferior and lateral portion of the postorbital plate, they do not provide evidence for the more superior part of the socket. In cranium 5, the postorbital plate is damaged inferiorly, but higher up along the back of the right socket (above the level of the zygomaticofacial foramen), the postorbital plate is complete and closed from lateral orbital rim to braincase wall (Fig. 5). Sutures are not evident, but the region coincides with where the zygomatic contacts the parietal bone in *Callithrix*. The superior broken edge of bone in cranium 5 apparently coincides with the frontal suture; the frontal bone has been displaced downward into the orbit (Fig. 5). The anatomical relationships seen in this specimen argue for direct zygomatic-parietal contact. This is further supported by the posterior portion of the temporal fossa in cranium 3, where one can make out the suture between the squamous part of the temporal bone and the parietal. The squamous temporal is positioned low enough on this specimen, and the frontal bone is positioned high enough on all the crushed crania, to hint that zygomatic-parietal contact may have occurred at the back of the orbit as in most platyrrhines (Fleagle and Kay, 1987).

Apart from postorbital closure, other details of the zygomatic bone are also of interest. There is a distinct zygomaticofacial foramen (= maler foramen), visible best on crania 1, 3, and 4 (diameter < 1.0 mm), which is proportionally larger than the pin-

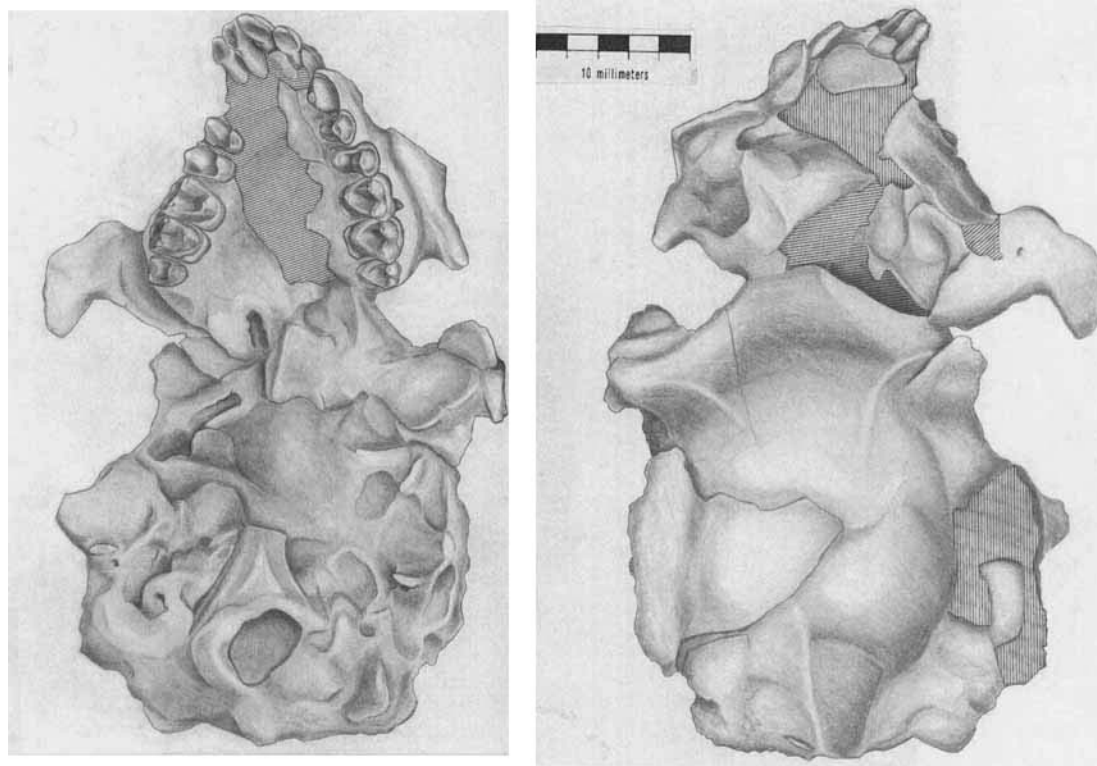


Fig. 3. Dorsal and ventral views of cranium 4 (DPC 11594). Dorsally (**right**), note the converging temporal lines and the posterior sagittal crest. Ventrally (**left**), note the dentition is intact except for the right canine, and that parts of the basicranium are preserved.

TABLE 1. Major cranial specimens of *Catopithecus browni*

ID no.	Museum no.	Figures	Notable features
1	DPC 8701	1	Sagittal crushing provides unique perspective on orbit and ear region
2	CGM 42222	1,6	In superior aspect, shows the least amount of overall shape distortion
3	DPC 11388	2,4,6	Best preservation of face, including nasals and premaxillae; basicranium partially preserved
4	DPC 11594	3,6,7,8,9,10	Dentition complete but for right canine; basicranium reasonably well preserved
5	DPC 12367	5	Well-preserved face and parts of vault; ventral parts damaged
6	CGM 41900	none	Immature cranium with well-preserved cheek teeth; shows partially fused metopic suture, canines not fully erupted

prick-sized foremen found in most catarhines, but it is not as large as the foremen in most platyrrhines, parapithecids, and adapoids (Oxnard, 1957; Hershkovitz, 1977; Gingerich and Martin, 1981; Fleagle and Kay, 1987). We do not detect evidence of a zygomatico-orbital foramen. The zygomatic-maxillary suture is discernible on the left

side of cranium 3. The suture runs diagonally from the inferior orbital rim to the base of the zygomatic arch. It specifically resembles this suture in *Callithrix* in that the orbital end of the suture is placed far medially (rather than laterally like in *Saguinus*) and the inferior end passes under the facial base of the zygomatic arch (rather than passing

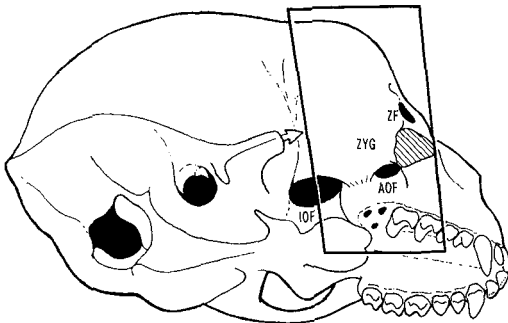
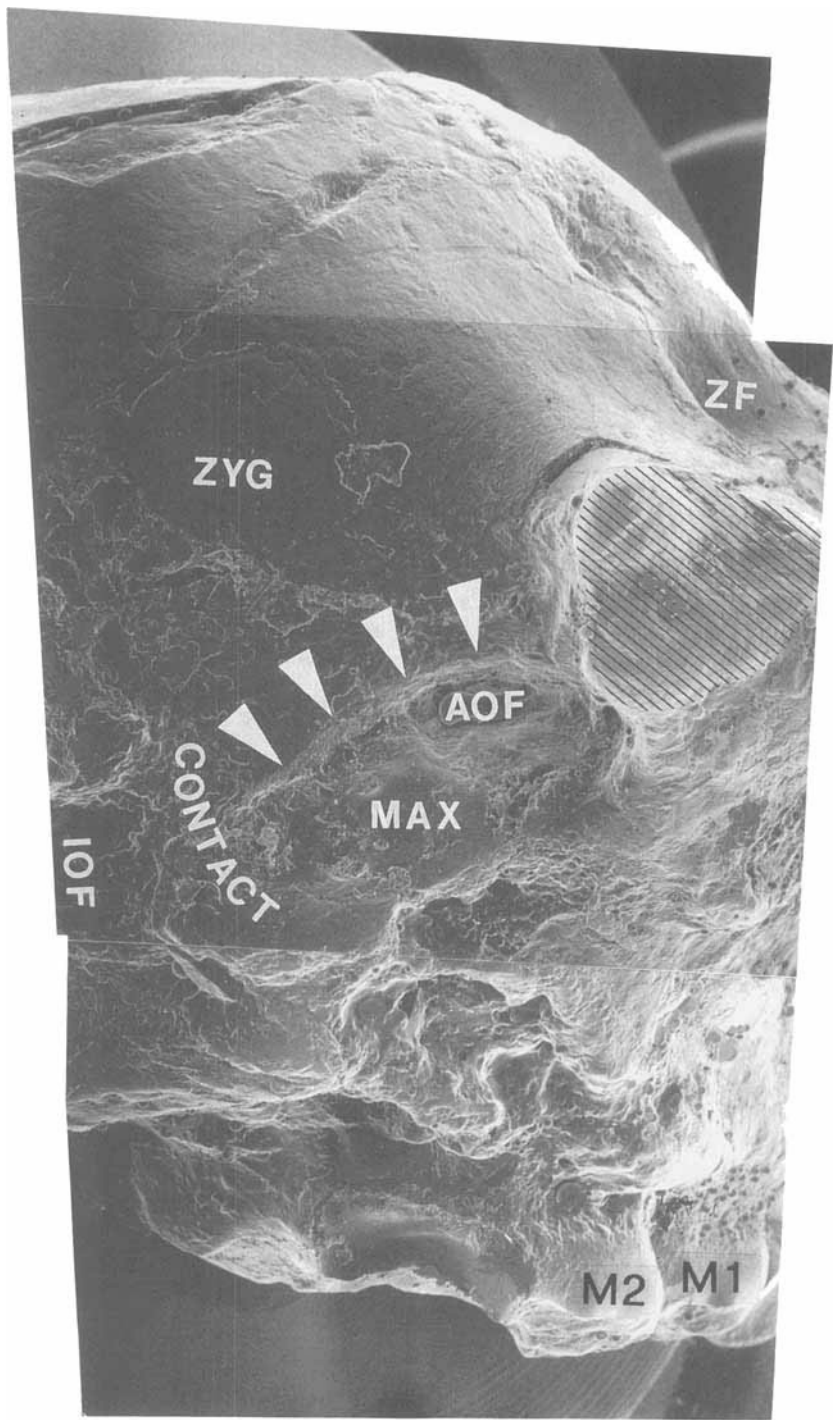


Fig. 4. Scanning electron micrograph (SEM) of the postorbital region of cranium 3. For help in anatomical orientation, the schematic drawing of a restored skull minus zygomatic arch shows the SEM picture outlined by a rectangle. The SEM shows the broad, cup-like post-orbital plate of the zygomatic bone, the inferior border of which is indicated by arrowheads; the broken base of the zygomatic arch (hatched); the maxillary tubercle and alveolar process with sockets for M^3 and posterolateral views of M^{1-2} crowns; and the seamless contact between zygomatic and maxilla, thereby secluding an anterior orbital fissure. AOF, anterior orbital fissure; IOF, inferior orbital fissure; MAX, maxillary tubercle; ZFG, zygomaticofacial foramen; ZYG, postorbital plate of the zygomatic bone.

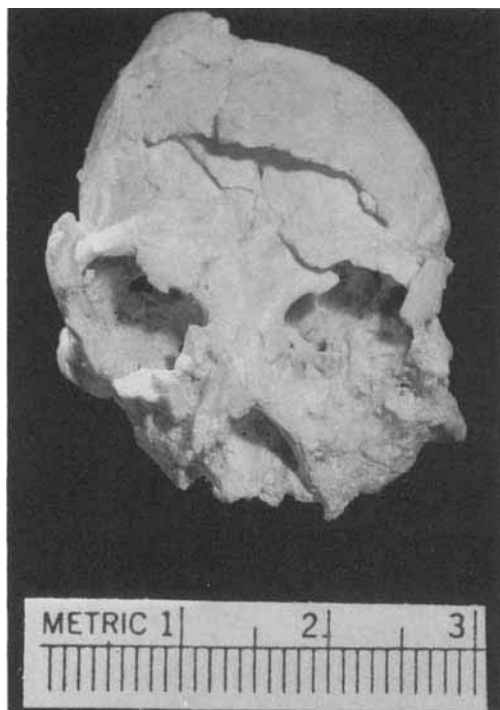


Fig. 5. Anterodorsal view of cranium 5 (DPC 12367) showing the well-preserved interorbital region, and the partially preserved orbits. Scale = 3 cm.

underneath at a point behind the facial surface like in *Saguinus*.

The orbital outline of *Catopithecus* shows a relatively sharp curve in its upper medial corner at the transition from horizontal plate of the frontal bone to the glabellar region (Simons, 1990); similar conformation is seen in several primates, notably *Apidium*, *Callicimico*, callitrichids, and cercopithecines. A supraorbital notch is evident on some specimens (e.g., crania 1, 3, 5; Fig. 5) but not others. The lacrimal foramen was intraorbital, as best viewed on cranium 5. A distinct anterior lacrimal crest is exposed on crania 3 and 5. Bone borders of the medial orbital rim and wall cannot be determined, due to breakage and poor exposure.

Orbit size of cranium 1 has been reported previously (Rasmussen and Simons, 1992). Additional data are now available from some of the other crania (Table 2). The new average values for orbit size (10.3 mm for mean of four individuals) and skull length (46.8

mm) fall very near the values of *Callithrix jacchus* when plotted on a bivariate analysis (Rasmussen and Simons, 1992), indicating that the orbits were proportionally small like those of modern diurnal primates. *Catopithecus* is within the range of small-bodied primates for which diurnality can be confidently differentiated from nocturnality on the basis of relative orbit size (Kay and Cartmill, 1977).

Orbit frontation cannot be measured due to crushing. However, it is possible to obtain estimates of orbital convergence from specimens that were crushed flat in a transverse plane. Two methods of obtaining the convergence angle were applied: the trigonometric approach of Lanèque (1993), and a simple graphic method using skull outlines and a protractor (Fig. 6). The assumption in using the latter method is that crushing in the transverse plane did not significantly alter the convergence angle as determined by medial and lateral bending points of the orbit rim. This assumption is supported by the observation that frontal bones are often preserved intact across the interorbital region. Using both methods, the values derived for *Catopithecus* indicate an animal with convergence of about 120–130°, within the high range for prosimians and the low range for anthropoideans (Table 3; Fig. 6).

Rostral region. *Catopithecus* had a broad, interorbital distance as exposed on the facial surface (Figs. 1, 2, 5, 6), comparable to those of some prosimians, callitrichids, colobines, and hominoids. Among anthropoideans, the interorbital regions of gibbons, colobines, callitrichids, and *Alouatta* are proportionally broader than the narrower interorbital regions of *Pongo*, *Cercopithecus*, and *Saimiri*. When evaluated in a bivariate plot of interorbital distance as a function of skull length, *Catopithecus* falls in the range of overlap between tooth-combed prosimians and callitrichids (the new data derived from several skulls yields a mean value that falls within the shaded range plotted by Rasmussen and Simons, 1992:497). It cannot be determined if *Catopithecus* had an interorbital septum farther back in the spheno-ethmoidal part of the interorbital region (Hershkovitz, 1977; Simons and Rasmussen, 1989).

TABLE 2. Skull measurements of *Catopithecus browni*

	Cranium number						Mean
	1	2	3	4	5	6	
Right orbit diameter	11.5	10.8	10.1	—	8.9	—	10.3
Left orbit diameter	—	11.0	—	—	8.3	—	9.6
Interorbital breadth	5.5	—	6.5	5.9	6.0	5.4	5.9
Biorbital width	—	28.7	24.7	—	—	—	26.7
Lanèque's (D3+D4)/2	—	15.4	14.1	—	—	—	14.8
Convergence (trig.)	—	137°	123°	—	—	—	130.0
Convergence (graphic)	—	120°	132°	120°	—	—	124.0
Nasal bone length	—	—	7.7	—	7.7	—	7.7
Prox. binasal width	—	—	3.8	—	3.9	—	3.8
Dist. binasal width	—	—	3.5	—	—	—	3.5
Foramen magnum length	—	5.2	—	6.0	—	—	5.6
Foramen magnum width	—	4.5	—	6.0	—	—	5.2
Molar series length	8.4	8.3	7.4	8.4	8.5	8.7	8.3
Premol. + molar length	13.5	12.8	12.1	13.4	—	13.8	13.1
Est. skull length	~45	~48	44	~50	—	—	46.8
Breadth across M ²	—	20.2	19.2	18.3	18.7	—	19.1
Bipostglenoid width	—	26.0	—	—	—	—	26.0

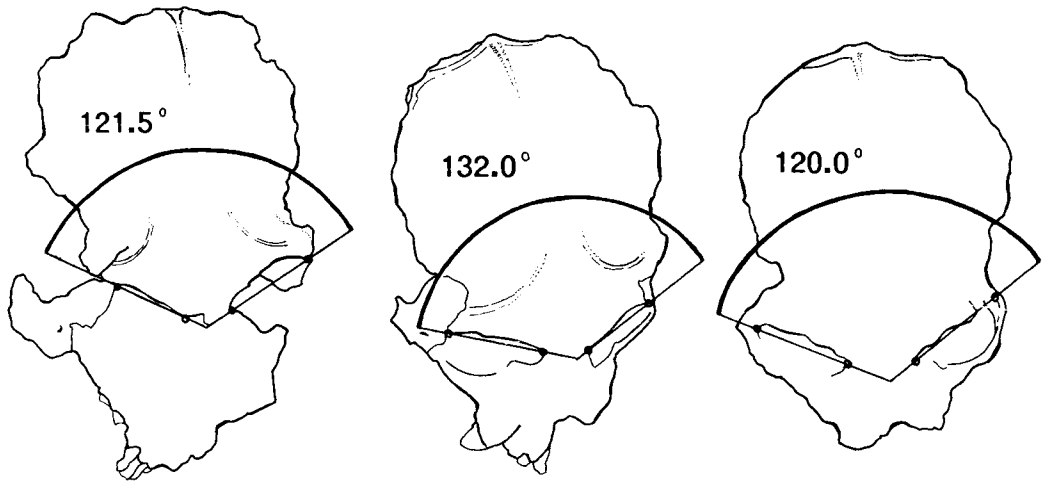


Fig. 6. Outlines of three crania of *Catopithecus browni* showing the angle of orbital convergence (from left to right, crania 4, 3, 2). In each case, the skulls are crushed flat, and thus the orbits have collapsed around a medial and lateral point of bending. The plane of each orbit was determined by drawing a line through the medial and lateral bending points, and the angle was determined by measuring the intersecting midline angle.

The nasal bones of cranium 3 and 5 are well preserved (Figs. 1, 2). These are proportionally broad and long (Table 2), like those of prosimians and callitrichids, rather than narrow like those of most cebids and cercopithecines. The rostral end of the nasals is pointed in cranium 3, leaving a notch between the two nasals to form the upper margin of the piriform aperture (nasals of cranium 5 are not pointed, but the tips are apparently broken). The nasal bones are

supported by a robust frontal process of the maxilla and a broad ascending ramus (= nasal process) of the premaxilla. Fleagle and Kay (1987) claimed that posteriorly expanding nasal bones are a prosimian trait in contrast to the allegedly anthropoidean condition found in *Apidium*, but examination of prosimians indicates that this is not the case. Most extant prosimian genera have nasals that do not broaden, or that sometimes narrow, to the back (*Lepilemur*, *Hapa-*

TABLE 3. Convergence angle of selected primates¹

Species	Convergence angle
<i>Eooticus elegantulus</i> ³	68
<i>Microchoerus</i> sp. ³	94
<i>Eulemur mongoz</i> ²	106
<i>Eulemur macaco</i> ²	108
<i>Eulemur fulvus</i> ²	108
<i>Varecia variegata</i> ²	111
<i>Avahi laniger</i> ²	112
<i>Adapis</i> sp. ³	114
<i>Propithecus verreauxi</i> ²	115
<i>Propithecus diadema</i> ²	117
<i>Indri indri</i> ²	118
<i>Adapis</i> sp. ³	120
<i>Catopithecus</i> , graphic method	124
<i>Rooneyia viejaensis</i> ³	126
<i>Catopithecus</i> , trigonometric method	130
<i>Perodicticus potto</i> ²	132
<i>Leptadapis</i> spp. ²	133
<i>Nycticebus coucang</i> ²	141
<i>Aegyptopithecus zeuxis</i> ³	142
<i>Adapis</i> spp. ²	149
<i>Papio hamadryas</i> ³	170
<i>Macaca hecki</i> ³	170
<i>Rhinopithecus roxellanae</i> ³	170

¹The reported angle is between the orbits, rather than between one orbit and a sagittal plane.

²From Lanèque (1993).

³From Ross (1994).

lemur, *Avahi*, *Propithecus*, *Galago*, *Loris*, *Nycticebus*, *Arctocebus*, *Perodicticus*, and *Tarsius*). Thus, the shape of the nasals of *Catopithecus* are not particularly informative with respect to higher level taxonomy.

Premaxilla and maxilla. The maxilla and premaxilla are particularly well preserved on both sides of cranium 3 and the left side of cranium 4. The maxilla is relatively deep and long compared to those of extant small-bodied platyrrhines. One of the most distinctive features of the face of *Catopithecus* is the very broad ascending process of the premaxilla. The premaxilla is nearly as broad at its superior (nasal) end as it is at the alveolar process (Fig. 7). The lateral margin of the piriform aperture can be assessed on crania 3 and 5; the margin originates inferiorly from the alveolar process as a smooth ridge, concave medially, and it pinches to a more sharp-edged ridge as it rises. Together with the pointed apex of the aperture between the nasal bones (cranium 3), this suggests a teardrop shape of the piriform aperture (cf. Hershkovitz, 1977:125).

The subnasal alveolar process is similar to those of callitrichids in shape, and appar-

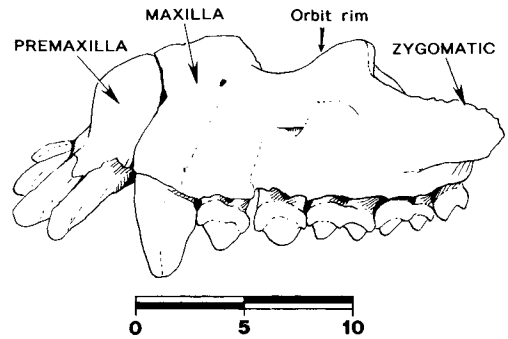


Fig. 7. Line drawing of the left side of the face of cranium 4, showing the relatively long and deep maxilla (frontal process missing), and the proportionally broad ascending wing of the premaxilla. Even in this relatively undistorted facial exposure, there has been some dorso-ventral crushing. The highly prognathic orientation of the incisors is partly the result of postmortem deformation. Scale bar = 10 mm.

ently in anatomical orientation. Two crania have incisors preserved, but they are somewhat displaced: In cranium 3, the two right incisors have been driven upward a few millimeters into the premaxilla; in cranium 4, the orientation of all four incisors has been flattened toward the transverse plane (Fig. 7). The central incisor alveolus is larger than the lateral one, and there is a diastema between the lateral incisor margin and the maxillary suture.

In cranium 4, the midline interincisal diastema at about the alveolar border is 0.8 mm. A mesial wear facet near the tip of the central incisors (Fig. 8) indicates that, like in adapoids and many anthropoideans, *Catopithecus* had midline contact of the spatulate incisors, and therefore, a small triangular opening between the bases of the central incisors. In the relatively narrow size of this opening, *Catopithecus* falls in the low range of anthropoideans (near the similarly sized *Callithrix*) and outside the range of the notharctines and adapines measured by Beard (1988).

The frontal process of the maxilla in *Catopithecus* is relatively broad. The anterior (medial) margin of the orbit is positioned above the contact between P³ and P⁴ (e.g., Fig. 7). Most small platyrrhines have the orbit positioned more anteriorly; catarrhines often have the medial orbit border positioned

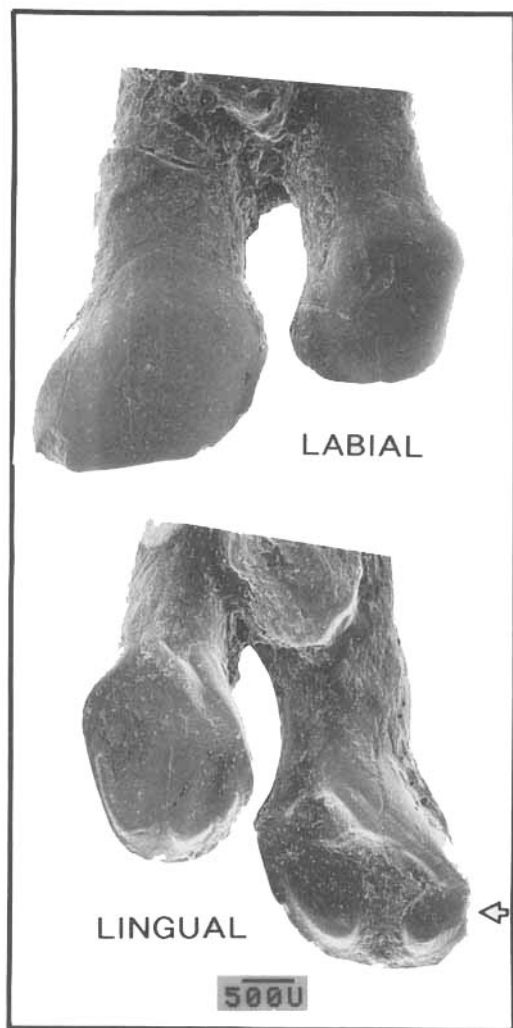


Fig. 8. Scanning electron micrographs of the left incisors of cranium 4 in labial view (**top**) and lingual view (**bottom**). Note the relatively flat-edged, flaring crown of I¹, the more ovate shape of I², and the flat mesial facet created by interstitial wear between right and left central incisors (viewed perpendicularly in the lingual view as indicated by the arrow).

above P³⁻⁴. A single infraorbital foremen is present, as seen in crania 1, 3, and 4, situated about 1.7–2.0 mm below the inferior orbital margin.

The maxillary alveolar process contains sockets for a canine, two premolars, and three molars. The canine root is proportionally large and sexually dimorphic. A distinct canine jugum and canine fossa are present. The

root of the zygomatic arch lines up above the M², 2.1–2.4 mm above the alveolar margin. The maxillary tuber is smooth and rounded like those of small platyrrhines. There is evidence of a maxillary sinus or sinuses exposed on the left side of cranium 4, but the details of this structure are damaged.

The right and left maxillary toothrows of *Catopithecus* apparently converge slightly toward the front, as in *Aegyptopithecus* and *Saimiri* (among other examples). Cranium 4 preserves the posterior edge of the left incisive foremen, but the size and shape of the foremen are obscured by crushing of the premaxilla into the region. The midline suture is also intact on this specimen from the level of the canine to P⁴. This allows the intercanine distance to be gauged, which is relatively broad like those of later anthropoideans (measured half distance = 3.0 on cranium 4; total distance = 7.4 on cranium 3). The pyramidal processes of the palatine bone are placed laterally and are robustly built, forming raised struts running diagonally from the palate in a posterolateral direction. In these features, *Catopithecus* closely resembles *Aegyptopithecus* and some catarrhines such as *Miopithecus* but differs from the proportionally less robust processes seen in most anthropoideans. The condition in *Catopithecus* differs substantially from the dorsally elevated, medially placed pyramidal processes of *Tarsius* and omomyids. The back edge of the hard palate is doubly concave in ventral view, arcing between posterior nasal spine and pyramidal process. In Cranium 2, two broken, thin plates of bone posterior to the pyramidal process represent slightly displaced bases of the medial and lateral pterygoid plates.

Upper dentition. The dentition is preserved on cranium 4 except for the right canine. The central incisors have long, straight, cylindrical roots. Proceeding apically from the cemento-enamel junction, the central incisor crown flares in the mesiodistal plane, forming a broad, spatulate crown (Fig. 8). The mesial edge of the crown is relatively straight and long, while the distal edge is more curved. The labial face is smooth and slightly convex; the lingual face is relatively flat. The labial-lingual thickness of the

crown decreases from base to occlusal edge. At the occlusal border, the crown forms a long, relatively flat, incisive edge. In overall structure, the tooth does not depart notably from those of small platyrrhines. The lateral incisor is morphologically similar to the central except for its smaller size, proportionally narrower crown, and rounded rather than flat occlusal edge, thus forming a more ovate outline. The lateral incisors are very similar to those of small platyrrhines.

The canine is a simple, caniniform tooth. It is larger than the other antemolar teeth in root diameter and crown height. In cross section, it is somewhat compressed side to side, but not to the extent seen in tooth-combed prosimians. On the mesial base of the crown there is a cingulum that can be followed around to the buccal side. A mesial groove, individually variable in intensity, extends from the cingulum two-thirds or more of the way to the apex (Gingerich, 1981a; Rasmussen, 1990). The wear facet for the lower canine extends from the mesial apex up both sides of the groove, especially the buccal side. On the distolingual edge of the upper canine is a wear facet for P_3 .

Specimens of *Catopithecus* show clear evidence of sexual dimorphism in canine size as documented in a number of different mandibular specimens (Simons, 1995b). The two best mandibles, a male (DPC 7342) and a female (DPC 11943), share the same molar series length (9.5 mm), but the canine of the male is substantially larger than that of the female in both crown height (4.6 vs. 3.7 mm) and root diameter (2.8×2.4 vs. 2.2×1.9 mm). The upper and lower anterior premolars are also affected by this dimorphism, being larger in males than in females.

The anterior premolar (P^3) has a single, large cusp positioned near the buccal margin of the tooth, two small styles on the mesio-buccal and mesiodistal borders of the tooth, and a small lingual lobe bearing a slight cuspule. Its structure is generally similar to the P^2 and P^3 of callitrichids. The posterior premolar (P^4) is notably larger than P^3 and has a proportionally larger lingual cusp and mesio-buccal style. The tooth is slightly waisted in occlusal outline; the lingual lobe is considerably smaller than the buccal one (Fig. 9).

The occlusal surfaces of the two anterior molars (M^{1-2}) have approximately equal-sized paracone, metacone, and protocone, and a smaller hypocone arising from a broad distolingual cingulum (Fig. 9). The preprotocrista swings mesio-buccally to the mesial margin of the tooth, while the postprotocrista arcs disto-buccally to the metacone. Together, the protocristae form a smoothly arcuate crest. Both molars show a slight mesostyle nodule and a faint buccal cingulum. The hypocone of M^2 is larger than that of M^1 . The second molar also has a distinct pericone on the cingulum immediately lingual to the protocone. The third molar is reduced in size; its metacone is small, and a hypocone is absent.

Tooth eruption

Two specimens of the upper dentition allow determination of the dental eruption sequence in *Catopithecus*. DPC 13604 has the upper canine, P^3 , and M^3 unerupted but preserved in the maxilla, while M^{1-2} are fully erupted in occlusal position. The P^4 root sockets indicate this tooth had erupted, but possibly not in full occlusion, with the tooth having fallen out postmortem. DPC 12367 has P^3 – M^3 erupted and in occlusion, but the canine apex is positioned just past the occlusal surface of the cheek teeth, and therefore not fully erupted. Assuming M^1 erupted before M^2 as in other primates, this indicates an eruption sequence of

$$M^1, M^2, P^4, (P^3, M^3), C.$$

This matches the mandibular eruption sequence determined for *Apidium phiomense*, except for the extra premolar of the latter species, which erupts (in timing) between M^2 and P^4 (Kay and Simons, 1983).

According to Kay and Simons (1983), late eruption of the canine is found only in adapoids and anthropoideans, not in strepsirrhines, tarsiers, or *Absarokius*. However, few data were then available concerning maxillary eruption in extant strepsirrhines. Smith et al. (1994) compiled raw data collected by R. Eaglen which show that in *Lemur catta* the canine is essentially tied with M^3 and P^2 as the latest erupting maxillary tooth (at 1.26 years). In *Varecia variegata*,

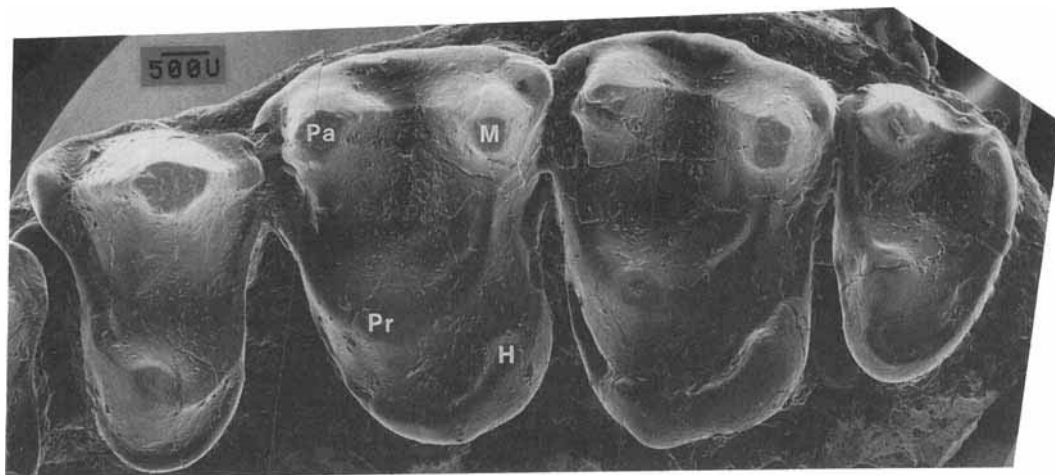


Fig. 9. Scanning electron micrograph of left maxillary P⁴-M³ from cranium 4. The primary cusps are labeled on M¹: H, hypocone; M, metacone; Pa, paracone; Pr, protocone. Compare to other early anthropoid and adapoid teeth (Rasmussen and Simons, 1988; Godinot, 1994); note especially the very close similarity be-

tween the M² of *Catopithecus* and that of *Periconodon huerzeleri* illustrated in a scanning electron micrograph published by Godinot (1994:250), from which *Catopithecus* differs in having a less distinct pericone and hypocone.

the mean canine eruption (1.16 years) is after mean M³ eruption (1.13 years), whereas in *Eulemur fulvus* the mean canine eruption (1.17 years) is before eruption of the premolars and M³ (1.19 to 1.21 years).

Among callitrichids (which lack M³) canine eruption is always last (Smith et al., 1994). Canine eruption is also last in *Aotus trivirgatus*, whereas canines erupt about the same time as M³ in *Saimiri sciureus*. Among extant catarrhines, M³ always erupts last, with the canine usually penultimate (Smith et al., 1994). In catarrhine species, P³ usually erupts before P⁴, whereas in platyrrhines, P⁴ usually precedes P³ (Smith et al., 1994). *Catopithecus* therefore resembles platyrrhines in the eruption of P⁴ before P³, and M³ before the canine. Because eruption sequence is related to the duration of development (Smith, 1989, 1992), this suggests that *Catopithecus* had a life history pattern similar to that of small platyrrhines, rather than those of relatively slowly developing extant catarrhines.

Braincase

Frontal. The ectocranial surface of the frontal bone is well preserved in most of the specimens. In all but one specimen, there

is no evidence of a metopic (= interfrontal) suture. One immature specimen with an unerupted canine (DPC 12367) has a metopic suture extending from the nasal border of the frontal bone to about the middle of the frontal. No suture is visible toward the back of the frontal bone. Total length of the visible suture is 8.5 mm of the approximately 15 mm length of the frontal bone. Frontal bones have been cracked near the midline in cranium 2 and DPC 11434, but these cracks do not follow precisely the line of metopic fusion.

Temporal lines of *Catopithecus* are arcuate, and are continuous anteriorly with strongly developed orbital crests positioned on the posterior edge of distinct supraorbital costae (Figs. 2, 3). Posteriorly, the temporal crests do not converge until near or beyond the back margin of the frontal bone. Thus, a frontal trigon is present, but it is relatively larger than that of *Aegyptopithecus*, *Apidium*, or *Victoriapithecus* (Simons, 1987; Benefit and McCrossin, 1993).

The midline profile of the frontal squama is perhaps best preserved in the sagittally crushed specimen (cranium 1), suggesting a very slightly domed forehead, as in *Calithrix*, but contrasting with the flatter pro-

file typically seen in *Saguinus* and the much higher, smoother dome of *Saimiri* and *Miopithecus*. A slight frontal dome is also evident on cranium 3 and DPC 11434.

The intracranial surface of the frontal bone can be examined in DPC 11434. There is a distinct frontal crest dividing the olfactory fossa into two halves. An anterior ethmoidal foramen (which transmits the nasal nerve and anterior ethmoidal vessels) is present bilaterally in the medial roof of the orbits. The size of the olfactory bulb is discussed below under the subheading for the brain.

Posterior braincase. The arcuate temporal lines meet posteriorly to form a low, midline sagittal crest, best evident in crania 2, 3, and 4 (Figs. 2, 3, 5). A distinctive feature of *Catopithecus* is the sharp nuchal crest at the back of the vault, and its associated prominent external occipital protuberance. It is evident that there was a distinct angle of the lateral cranial profile at the crest, such that the nuchal plane is flatter and more vertically oriented than the arched cranial vault anterior to the crest. (An apparent, soft ridge at the back of the preserved vault in cranium 5 is an artifact of postmortem bending, as the ridge lies too far forward to really correspond to the lambdoid region.) The distinct cresting that lies at the posterior edge of the vault in *Catopithecus* suggests no ballooned expansion of the occipital region such as is found typically in callitrichids and small cebids. Rather, the posterior cranial profile was somewhat truncated, with a relatively flat, vertical nuchal plane in comparison to extant small anthropoids, perhaps similar to the cranial profile of *Alouatta*.

The brain. Among all the skull specimens, cranium 2 is the one that most nearly preserves the general outline of the braincase (Fig. 1). After correcting for apparent distortion caused by being shattered and flattened, a brain model can be prepared in clay that represents an approximate volume of the brain. The braincase itself in marmoset-sized primates is eggshell thin, and therefore, there is little difference between endocranial volume and ectocranial volume. Upon immersion in water, the clay model dis-

TABLE 4. Encephalization quotient estimates for *Catopithecus browni*¹

Body weight estimates	Brain size estimates		
	2.8	3.1	3.4
400 g	0.42	0.47	0.51
600 g	0.32	0.36	0.39
800 g	0.26	0.29	0.32

¹EQ = (brain size estimate)/(10^{log}body size estimate)^{0.67-0.92}, or EQ = (brain size estimate)/(0.12)(body size estimate)^{0.67}.

TABLE 5. Encephalization quotients of fossil primates

Genus	Radinsky (1977)	Jerison (1979)	Conroy (1987) ¹
<i>Tetionius</i>	0.42	0.71	0.35
<i>Necrolemur</i>	0.79	0.94	—
<i>Rooneyia</i>	0.97	1.23	—
<i>Adapis</i>	0.39	0.53	0.98
<i>Smilodectes</i>	0.41	0.53	0.55
<i>Aegyptopithecus</i>	—	0.97	0.78
<i>Proconsul</i>	—	—	1.89
<i>Oreopithecus</i>	—	—	4.77

¹These values use body weight estimates derived from Conroy's "all primate" regression. Conroy noted that variation in body weight estimates, not brain size estimates, are responsible for the greatest variation among EQ estimates.

placed 3.1 cm³ (Simons, 1995b), a size that seems consonant with other specimens, such as crania 3 and 5. Using the dimensions of the foramen magnum (Table 2) to estimate brain size (Gingerich and Martin, 1981) yields an even smaller estimate for the brain of *Catopithecus* (2.4 cm³), which seems too small for the observed vault size.

Hypothetical encephalization quotients (Table 4) can be calculated for *Catopithecus* given a range of body weight estimates and the brain size estimate of 3.1 cm³ ± 10% (2.8–3.4 cm³). The values obtained for *Catopithecus* are in the lower end of the range reported for some other Eocene primates (Table 5). Compared to modern primates, the brain size estimated for *Catopithecus* is extremely small. For example, extant species with brains as small as 3–3.5 cm³ (Stephan et al., 1981) include some of the smallest prosimians, which are much lighter than the estimated body weight of *Catopithecus* (e.g., *Cheirogaleus medius*, body weight ~200 g; *Galago demidoffi*, body weight < 100 g).

The size of the olfactory bulb can be assessed using latex pulls from an isolated frontal bone (DPC 11434). The fossa for the bulb measures between 4 and 5 mm long,

and is about 4 m wide. In absolute size and in proportion to the facial cranium, this is about the same size as latex pull from a frontal bone of *Apidium phiomense* (Simons, 1959). The size of the olfactory bulb in *Apidium* has been characterized as prosimian-like (Hofer, 1962), or as intermediate between the typical prosimian and anthropoidean conditions (Radinsky, 1974; Fleagle and Kay, 1987). The olfactory bulbs of both *Catopithecus* and *Apidium* are relatively larger than that of *Aegyptopithecus* (Radinsky, 1973). *Aotus* has the largest olfactory bulb among extant anthropoideans, followed by callitrichids (Stephan and Andy, 1969). The olfactory bulb of *Catopithecus* projects in front of the frontal lobe, like prosimians, but unlike extant anthropoideans. Radinsky (1973) reported that the olfactory bulb projected anteriorly in *Aegyptopithecus*, but more recently it has been shown that the projection was downward (Simons, 1993).

Basicranium

Basioccipital. The basioccipital of *Catopithecus* can be best seen in cranium 4, where it has come loose from the basisphenoid and from the left petrosal (Fig. 3). The basilar part of the occipital is comparable in its proportions to those of small platyrrhines (which contrast sharply with the extremely narrow one of *Tarsius*). There are no flanges evident on *Catopithecus* that would overlap the auditory region. The occipital condyles are typical of those found in anthropoideans and most other primates: The articular surface broadens posteriorly and gently shifts from a lateral orientation to a more ventral orientation; the posterior part of the articular surface has a definite flexure, or convexity downward (for flexion and extension of head on neck). This morphology contrasts with the condition in *Tarsius*, in which the articular surface remains laterally oriented from front to back, does not widen, and lacks the characteristic convexity (thereby emphasizing a pivoting movement of the head on the neck). The foramen magnum is positioned near the back of the cranium compared to small platyrrhines and tarsiers, but it is forward compared to most prosimians. The jugular process is evident on cranium 3, where it overlaps the mastoid portion of

the temporal bone. A posterior lacerate foramen is evident along the occipital border with the temporal bone, but details of shape and size are lost to damage.

Auditory region. The temporal bone of *Catopithecus* is best visible in crania 1, 3, and 4. There was no tubular ectotympanic. Instead, crania 1 and 3 each show the auditory meatus surrounded by an elevated rim that represents the ectotympanic (Simons, 1990). A small fragment of temporal bone (DPC 11434) preserves a broken cross section of the ectotympanic ring where it has snapped off at the anterior curve of the external acoustic meatus. Thus, the ectotympanic was an annular structure fused to the lateral margin of the bulla, as in platyrrhines and *Aegyptopithecus*.

Some details of the petrosal part of the temporal can be seen on both sides of cranium 3 and the right side of cranium 4. In the process of being crushed, cranium 3 had the left temporal bone in its entirety (squamous part included) folded across the underside of the specimen and then pressed flat. The squamosal suture is visible about 5.0 mm above a strong suprameatal crest, which is continuous anteriorly with the zygomatic process. The exposure of the mastoid is clearly delimited on the left side, but its surface is shattered. The postglenoid process is a well-preserved landmark.

A postglenoid foramen is present immediately behind the postglenoid process (not medial to it as in *Tarsius*). The postglenoid foramen is greatly reduced or absent in modern catarrhines, is present and variable in size among platyrrhines, and is present in most prosimians. Hershkovitz (1977) reported the foramen was consistently large in *Leontopithecus* and *Cebus*, while it was obsolete or absent in *Callicebus* and in most individuals of *Callimico*. The presence of a postglenoid foramen has also been reported in *Aegyptopithecus* (Simons and Rasmussen, 1989); its occurrence in the two early Fayum catarrhines indicates that its reduction or loss has occurred in parallel between catarrhines and some platyrrhines.

The right temporal bone of cranium 3 is preserved fairly well posteriorly and laterally, but it is badly damaged anteriorly and

medially. The mastoid portion is well exposed; as on the left side, its surface is delicate and fragmented, in contrast to the smooth, firm surface of the bordering occipital bone and the acoustic meatus. This indicates that the mastoid was inflated by air cells and superficially covered by a relatively thin outer table. The outline of the auditory meatus is discernible on the right side of cranium 3, although it is broken in places. The middle ear spaces and their contents are badly crushed except posteriorly.

The jugular fossa at the border of the occipital and temporal is preserved on this side. A hypoglossal canal is present against the base of the occipital condyle. The seam between the occipital and temporal bones for the posterior lacerate foramen is pressed shut (postmortem). Lateral to the jugular fossa, opening out of the posteromedial slope of the bulla is the posterior carotid foramen, its formerly round outline distorted and partially closed. Thus, the entry of the carotid is posteromedial, near the rim of the jugular fossa. In the positioning of structures in the region of the jugular fossa, *Catopithecus* closely resembles the arrangement seen in *Aegyptopithecus*, *Miopithecus*, small platyrrhines, and many other anthropoids (*Homo* being one exception).

The right temporal bone of cranium 4 has been folded and crushed at the suprameatal crest. Thus, the squamous part is visible on the superior surface of the specimen, while the petrous part is visible inferiorly. The postglenoid process and foramen are preserved in this specimen. The posterior portion of the auditory bulla has been stripped away, revealing the tympanic cavity and promontorium (Fig. 10). The round window (= *fenestra vestibuli*) is clearly exposed, and can be used as a central point of reference. The oval window (= *fenestra cochlearis*) is hidden from view because the cochlear housing has been crushed into the roof of the tympanic cavity. On the back rim of the tympanic cavity, posterolateral to the round window, is the stylomastoid foramen. A poorly defined mound of disordered bone behind the stylomastoid foramen apparently consists of surface mastoid fragments crushed over the resistant housing of the semicircular canals.

The unmistakable bony course of the

promontory canal is visible across the promontorium just anteromedial to the round window. Its distal terminus is broken away with the rest of the ventral bullar features. The posterior carotid foramen could only have been in the shallow fossa anterolateral to the jugular foramen. This position is consistent with the foramen preserved in cranium 3. Anteriorly, the promontory canal rides the anterolateral portion of the promontorium. A fairly large exposure of the anterior promontorium is visible medial to the promontory canal. The rough outlines of the anterior part of the bulla can be discerned; it appears to have been moderate in size and rather elongate, as in *Aegyptopithecus*. The foramen ovale is evident just outside the anterolateral margin of the petrosal at the base of the entoglenoid process.

The entire auditory part of the petrosal is similar to those of small anthropoids in those features that can be discerned. The one greatest difference from a small catarrhine such as *Miopithecus* is the lack of a tubular ectotympanic. The auditory region of *Catopithecus* also closely resembles YPM 23968, a temporal fragment attributed to *Apidium* (Cartmill et al., 1981). In the few details that can be discerned, *Catopithecus* did not differ appreciably from *Callithrix* in any aspect of shape, in the position of the carotid system, or in the relationships of the auditory apparatus to adjacent structures of the occipital bone and the temporomandibular joint. The one slight difference that is apparent, but which may be due in part to the pattern of crushing, is that the anterior portion of the promontory canal is positioned slightly lateral to its position in the small platyrrhines we have examined (or conversely, the anterior portion of the promontorium is more medial). The internal acoustic meatus and a larger, rounded subarcuate fossa (Straus, 1960) are evident on a small endocranial fragment of the petrosal associated with DPC 11434.

Temperomandibular joint. The temporomandibular joint is preserved very well in several specimens. In shape, it is relatively flat and broad (Simons, 1990). There is a slight, transverse furrow at the back of the articular surface, corresponding to the

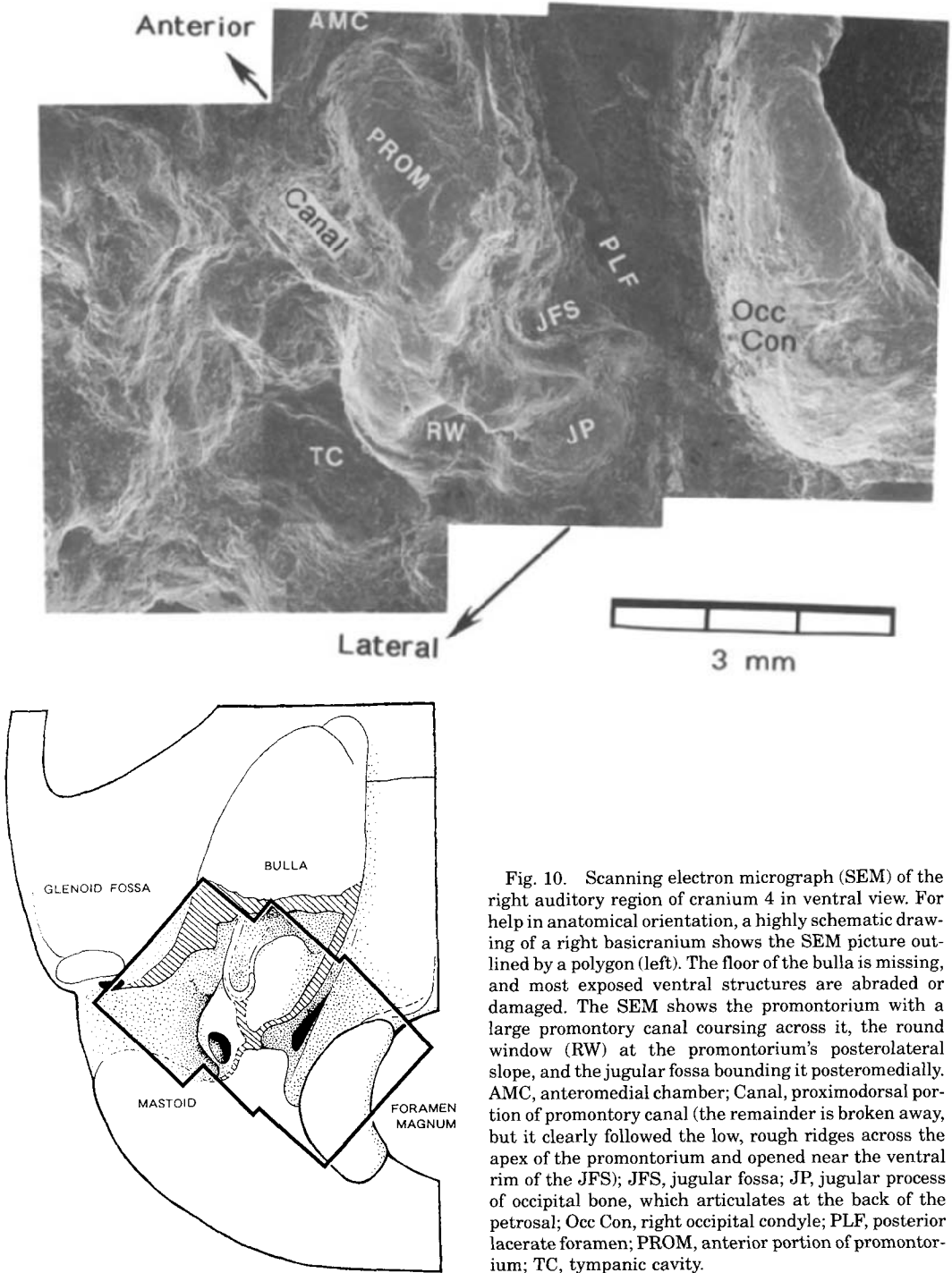


Fig. 10. Scanning electron micrograph (SEM) of the right auditory region of cranium 4 in ventral view. For help in anatomical orientation, a highly schematic drawing of a right basicranium shows the SEM picture outlined by a polygon (left). The floor of the bulla is missing, and most exposed ventral structures are abraded or damaged. The SEM shows the promontorium with a large promontory canal coursing across it, the round window (RW) at the promontorium's posterolateral slope, and the jugular fossa bounding it posteromedially. AMC, anteromedial chamber; Canal, proximodorsal portion of promontory canal (the remainder is broken away, but it clearly followed the low, rough ridges across the apex of the promontorium and opened near the ventral rim of the JFS); JFS, jugular fossa; JP, jugular process of occipital bone, which articulates at the back of the petrosal; Occ Con, right occipital condyle; PLF, posterior lacerate foramen; PROM, anterior portion of promontorium; TC, tympanic cavity.



Fig. 11. Left mandible showing unfused symphysis (DPC 7342). Note the rugose symphyseal surface. The central incisor is missing.

greatest depth of the glenoid fossa. The articular eminence is very slightly convex ventrally. A moderate entoglenoid process is present. There is no approximation toward the deep glenoid fossa and longitudinally guttered articular eminence seen in tarsii-form primates (Rosenberger, 1985).

Mandible

Symphysis, corpus, and ascending ramus. The mandibular symphysis is unfused (Ravosa and Hylander, 1994), even in adults with occlusal wear on their molars (Fig. 11). Specimens that preserve the symphyseal surface are the following (DPC 7341, 7342, 9869, 11388, 11541, 11638, and 11943). The symphyseal surface is covered with small, rugose ridges, reminiscent of the texture seen in juvenile individuals of *Archaeolemur* before fusion of the symphysis (Ravosa and Simons, 1994).

The mandibular corpus of *Catopithecus* is of about equal depth throughout the length of the toothrow, being only slightly deeper

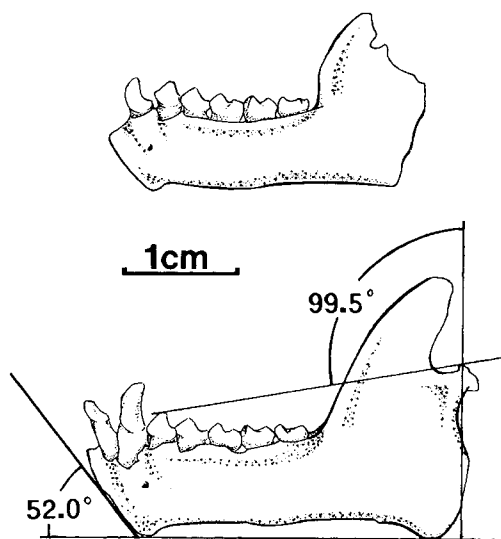


Fig. 12. Line drawings of two mandibles of *Catopithecus browni* drawn to same scale. Top: Female specimen (DPC xxxx) preserving C to M₃. Bottom: Well-preserved male specimen (DPC 7342) with I₂ to M₃. The angle of condylar suspension (99.5°) is illustrated for the male specimen. The symphyseal outlines of both mandibles are also illustrated.

anteriorly near the symphysis in at least one male specimen (Fig. 12). There is a single mental foramen between the roots of the canine and P₃. The ascending ramus rises steeper than a 45° angle to the corpus. The condylar process is well above the toothrow, yielding a value of condylar suspension that is similar to that of *Saimiri* (Fig. 12; Hershkovitz, 1977). The coronoid process is relatively very high, narrow, and vertical, without much of a superior curve backward. The gonial angle is slightly pointed, but it is not extended into a prominent angular process. Apart from the unfused symphysis, the mandible is very close in morphology to that of *Saimiri*, and contrasts with those of other small platyrrhines (e.g., *Callithrix*, *Saguinus*, *Callicebus* and *Aotus*).

Mandibular dentition. The lower teeth have been described and illustrated elsewhere: Simons (1989) used the lower teeth to diagnose the genus *Catopithecus* and to distinguish it from *Oligopithecus*; Rasmussen and Simons (1992) commented on functional aspects of the lower dentition; Simons

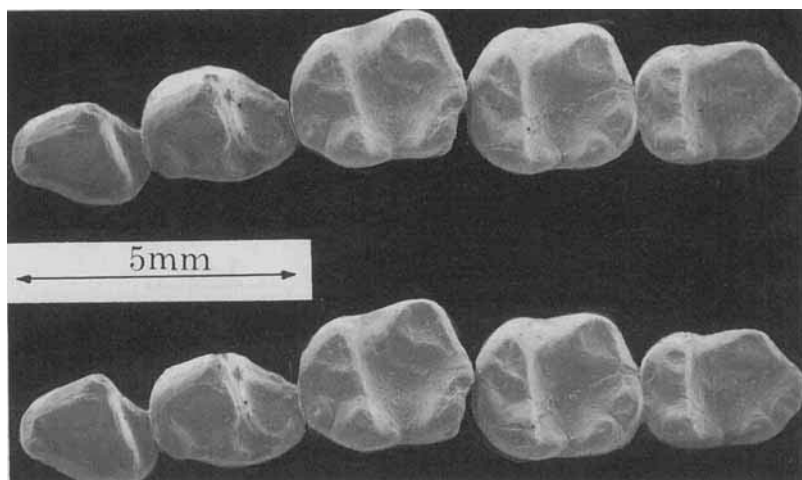


Fig. 13. Stereopairs of the mandibular cheek teeth (CGM 41885, the holotype). Note the anterior honing blade on P_3 , the development of a paraconid, metaconid, and talonid basin on P_4 , the complete trigonid of M_1 , the reduced trigonids of M_{2-3} , and the closely appressed entoconid-hypoconulid pair.

(1995b) reported on the canines and lower incisors. A few general points about the lower teeth are reviewed here.

The incisors are like those of modern anthropoideans in their spatulate shape and relative size proportions. The lateral incisor has a flat occlusal edge and straight mesial border, while the lateral border is sloping and bears a small distal nubbin. The canine is a large, projecting tooth that is sexually dimorphic in size (see above). The P_3 is a high-crowned tooth, with the leading edge forming a honing blade against the upper canine (Fig. 13). There is a slight talonid shelf. In males, P_3 is notably broader with a longer honing blade than in females. The P_4 is a more complex tooth than P_3 , bearing a small paraconid and metaconid, and a small but distinct talonid basin (Herskovitz, 1981). The first molar retains a distinct paraconid, which is slight or absent on M_{2-3} . The entoconid and hypoconulid are tightly twinned on all three molars. The lingual cusps are relatively bunodont, while the buccal ones are more cristiform.

DISCUSSION

Aegyptopithecus and *Apidium*

Catopithecus differs from *Aegyptopithecus* in several ways besides body size and dental occlusal features. Compared to *Aegypto-*

pithecus, *Catopithecus* lacks mandibular fusion, has a proportionally larger olfactory bulb, and has lighter cranial cresting. The temporal lines of *Catopithecus* converge much further back on the vault than do those of *Aegyptopithecus* (Simons, 1987). In both genera, temporal line position appears to be subject to much intraspecific variation that is partly related to age and sex, but all specimens of *Catopithecus* have less convergent temporal lines than all specimens of *Aegyptopithecus*. This morphological difference may be an allometric correlate of the size disparity between the two genera.

In contrast to the differences between *Catopithecus* and *Aegyptopithecus*, there are also some special similarities that are not typically found among later anthropoideans. Both Fayum genera have distinct supraorbital costae and slightly depressed glabellar regions; this construction also seems characteristic of Miocene anthropoideans (Leakey et al., 1991; Benefit and McCrossin, 1993). *Catopithecus* and *Aegyptopithecus* also share unusually deep, robust faces for animals of their sizes. *Catopithecus* and *Aegyptopithecus* both have relatively small encephalization quotients (EQ) in relation to later anthropoideans, with the EQ of *Catopithecus* apparently being the smallest of the two. This establishes that the larger brain and

reduced olfactory bulb that characterize extant catarrhines and platyrrhines have been acquired in parallel.

Catopithecus and *Aegyptopithecus* also share unusually broad ascending wings of the premaxilla. Although this could possibly be interpreted as a primitive retention from an adapoid ancestor, Simons (1972) pointed out that the ascending wing of the premaxilla in *Aegyptopithecus* "is so broad from front to back that it exceeds in relative size the proportions of this bone in most if not all Eocene primates." Catarrhines tend to retain broader premaxillae than platyrrhines. According to Herskovitz (1977), the articulation of the premaxilla in the two anthropoid groups differs; the ascending process just meets the lateral corner of the nasal bones in most platyrrhines, but is a thin slip extending between the distal nasals and the maxilla in most cercopithecoids. *Aotus* and callitrichids have the broadest ascending process among platyrrhines, and the greatest nasal-premaxillary contact (Herskovitz, 1977). Whether the broad ascending process of *Catopithecus* and *Aegyptopithecus* is a primitive retention from an ancestor with a large rostrum, or a peculiar specialization of propliopithecids or early anthropoids in general, cannot be resolved at present.

The posterior carotid foramen of *Catopithecus* is medially positioned near the jugular fossa, rather than more laterally as illustrated for *Aegyptopithecus* based on an incomplete auditory region (Simons and Rasmussen, 1989). New examination of the auditory region of the original 1966 skull of *Aegyptopithecus* suggests that the posterior carotid foramen was positioned more medially in this genus, too, like it is also in *Saimiri* and *Miopithecus*. In all three forms, a laterally placed promontory canal connects to a more medially placed posterior carotid foramen by way of a notable curvature of the distal carotid canal. The condition of the carotid system in *Catopithecus* and *Aegyptopithecus* is probably similar to that of *Apidium* (Gingerich, 1973; Cartmill et al., 1981; Simons and Rasmussen, 1989).

Although incompletely known, the facial structure of *Apidium* appears generally similar to that of *Catopithecus*. *Apidium* differs

from *Catopithecus* in the retention of second premolars. Some individuals of *Apidium* have a smaller trigon on the frontal bone than *Catopithecus* does, with the temporal lines converging more anteriorly on the cranial vault. The supraorbital costae of *Catopithecus* are more prominent than those of *Apidium*. *Apidium* retains a much larger zygomaticofacial foramen than *Catopithecus*, as in adapoids and many platyrrhines (Fleagle and Kay, 1987).

Catarrhines

Besides details of dental structure shared between *Catopithecus* and propliopithecines, there is no really compelling cranial evidence to classify *Catopithecus* as a catarrhine other than the loss of maxillary second premolars. Cranial features that may align *Catopithecus* specifically with the catarrhine *Aegyptopithecus* are the broad ascending process of the premaxilla and the reduced zygomaticofacial foramen. The large premaxilla may be a primitive retention from an adapoid ancestor. The occurrence of a zygomaticofacial foramen is uncommon in many mammal groups, but it is widespread, although variable in size, among primates. The foramen is "consistently larger in platyrrhines than in catarrhines of comparable skull size" (Herskovitz, 1977), and it is also large in *Apidium* (Fleagle and Kay, 1987), still larger in *Parapithecus* (Simons, 1995a), and large also in some adapoids (Gingerich and Martin, 1981). The zygomaticofacial foramen is absent in *Tarsius*. The infraorbital foramen of any given catarrhine is typically larger than its zygomaticofacial foramen, opposite the normal situation in platyrrhines. *Catopithecus* has these two foramina of similar size (cranium 3) or the catarrhine condition of having a larger infraorbital foramen (crania 1, 4). If the enlarged foramen found in platyrrhines, parapithecids, and adapoids is primitive for anthropoids, the reduction seen in *Catopithecus* and *Aegyptopithecus* may be a shared catarrhine specialization.

Apart from the dental formula, the main argument that *Catopithecus* was a catarrhine derives from dental continuities seen between it and other propliopithecids, linking *Catopithecus* through reasonable inter-

TABLE 6. Dental changes among propliopithecines within the Jebel Qatrani Formation, to be read from oldest (bottom) to youngest (top)

Taxon	Chron ¹	Dental features
<i>Aegyptopithecus zeuxis</i> and <i>Propliopithecus chirobates</i>	C13n	Honing edge of P ₃ lengthened Distal fovea becomes larger Molar hypoconulid shifts centrally Acute crests lost entirely Hypocone size becomes large Molar trigonids reduced in height Wear facet "X" appears M ₁ paraconid lost Distal fovea attains moderate size Increasing molar bunodonty
<i>Propliopithecus markgrafi</i> ²	C13r	Increasing molar bunodonty
<i>Oligopithecus</i> sp. nov. (Oman)	C13r	P ₄ trigonid closed M ₂ paraconid lost Slight distal fovea appears Increasing molar bunodonty
<i>Oligopithecus savagei</i>	C13r	Catarrhine dental formula
<i>Catopithecus browni</i>	C15r	

¹ Paleomagnetic data from Thomas et al. (1989); Kappelman et al. (1992).

² The geological source of the holotype and only known Fayum specimen of *P. markgrafi* is unknown; material referred to this species is from Taqah, Oman (Thomas et al., 1989, 1991).

mediates (*Oligopithecus savagei*, *Propliopithecus* spp.) to *Aegyptopithecus* (Table 6). Additional points of similarity have been noted in postcrania assigned to *Catopithecus* and propliopithecines (Gebo et al., 1994). The retention of many primitive features no longer found among extant catarrhines—such as the presence of a raised, complete trigonid, and the absence of mandibular fusion—may make these early anthropoids seem too primitive to be catarrhines, but it is becoming clear that a large number of primitive retentions would have to be found near the common ancestry of the major anthropoid clades (Fleagle and Kay, 1987). To reject *Catopithecus* from Catarrhini, one must explain how two-premolar primates that are not really catarrhines just happened to serendipitously form an apparent size and morphological sequence that coincides with the age sequence in the Jebel Qatrani Formation. We accept that *Catopithecus* is plausibly a true catarrhine, postdating the catarrhine–platyrrhine split.

It is now clear that a broad interorbital distance characterizes primitive catarrhines. This conclusion is based on the study of all available early catarrhine faces, including *Catopithecus*, *Aegyptopithecus*, *Victoriapithecus*, and Miocene hominoids (Simons and Rasmussen, 1989; Rasmussen and Simons, 1992; Benefit and McCrossin, 1993). Later reduction of interorbital distance in cercopithecines and some hominoids is a de-

rived condition. Other cranial features of *Catopithecus* that are of interest to help establish character polarity among catarrhines are the following: deep and moderately long maxilla; broad ascending wing of premaxilla; small, tamarin-like incisors; simple premolars; molars subquadrate with only a small hypocone; postorbital closure within the range of modern anthropoids, retaining an anterior orbital fissure in at least some specimens, and showing zygomatic-maxillary contact at the maxillary tuber; moderate-sized zygomaticofacial foramen; moderately pronounced supraorbital costae; posterior sagittal crest; pronounced external occipital protuberance; posteriorly developed sagittal crest.

Benefit and McCrossin (1991, 1993) have reconstructed a hypothetical ancestral facial morphotype for the clade containing extant catarrhines. A comparison of their morphotype to the face of *Catopithecus* (Table 7) suggests the evolutionary changes that have occurred during the approximately 10-million-year span between a basal catarrhine (postdating the split from platyrrhines) to an early modern catarrhine (near the common ancestry of extant forms). An interesting outcome from the comparison between small *Catopithecus* and the moderate-sized morphotype, and also from the comparison of moderate-sized *Aegyptopithecus* to large-bodied *Afropithecus* (Leakey et al., 1991), is that the early catarrhine face retained

TABLE 7. Comparison of *Catopithecus* to morphotype of ancestral modern catarrhine

Cranial character	Morphotype state (Benefit and McCrossin, 1993)	<i>Catopithecus</i> (this study)
Interorbital distance	Broad	Broad
Supraorbital costae	Present	Present
Frontal trigon	Present, restricted	Present, broad
Frontal bone orientation	Steep	Uncertain
Snout length	Moderate	Moderate
Nasal aperture shape	Oval or teardrop	Teardrop
Nasal bone shape	Long and narrow	Long, moderately broad
Facial height	Moderate to deep	Moderate to deep
Cheek height	Deep ("tall")	Relatively deep
Zygomaticofrontal suture	High	Indeterminate
Premaxilla shape	Long and tapering	Long and broad

many conservative features of shape despite undergoing substantial changes in size through time.

Platyrrhines

Catopithecus differs from most cebids in its much broader middle portion of the upper face. The breadth of frontal glabella, the large interorbital distance, the width of the nasal bones, and the more vertical (less medially inclined) frontal processes of the maxilla are all manifestations of this phenomenon. In these respects, *Catopithecus* is similar to callitrichids or *Alouatta*. The broader interorbital region of callitrichids persists only near the facial surface; deeper between the orbits, callitrichids have an interorbital septum. The nasal aperture itself is not relatively broader in callitrichids than in cebids, and the intercanine distance is not proportionally broader. Thus, the broad midface of callitrichids is apparently an "olfactory tube" passing from brain to nasal fossa associated with relatively large olfactory bulbs when compared to most anthropoideans (Stephan and Andy, 1969). We have interpreted the broad interorbital facial exposure of *Catopithecus* to be an adaptation for greater olfactory capabilities (Rasmussen and Simons, 1992), based on analogy to the olfactory system and scent-marking behaviors of callitrichids (Epplé, 1985, 1986; Epplé et al., 1987; Bartecki and Heymann, 1990).

In the structure of the lower face, *Catopithecus* departs from all the small-bodied platyrrhines. The rostrum of *Catopithecus* was somewhat longer and more heavily built than those of callitrichids, *Saimiri*, *Aotus*, and *Callicebus*. This is reflected in its longer

maxilla and its unusually broad ascending process of the premaxilla. Catarrhines typically have larger facial parts of the skull than platyrrhines (Ankel-Simons, 1983). The facial proportions of *Catopithecus* are fairly similar to those of *Alouatta* and *Aegyptopithecus*. The resemblances between the latter two in some aspects of cranial shape has been discussed previously (Radinsky, 1973; Simons and Rasmussen, 1989).

Another important disparity between *Catopithecus* and the small-bodied platyrrhines is in relative brain size. Although this variable cannot be measured directly in the broken Fayum specimens, all structural features relating to cranial cresting, foramen magnum position and size, and overall size of the crushed outlines of the braincase prove that *Catopithecus* had a relatively smaller brain than modern platyrrhines of similar body size.

In contrast to the small-bodied platyrrhines, *Catopithecus* resembles *Alouatta* in its heavier face, its proportionally smaller brain, more pronounced cranial cresting, and probably in its facial profile. Thus, if shared features of *Catopithecus* and extant platyrrhines reflect the structure of the ancestral platyrrhine, these animals were hypothetically similar in size to callitrichids but perhaps with the primitive muzzle, relatively smaller braincase, and more pronounced posterior cranial cresting resembling these features as seen in *Alouatta*.

Tarsiers

Tarsiers have traditionally played an important role in theories of anthropoidean origins (Wortman, 1903; Jones, 1929; Cartmill, 1980, 1994; Rasmussen, 1994). Indeed, one

TABLE 8. *Catopithecus browni* compared to *Tarsius* and *Adapidae*¹

Feature	<i>Tarsius</i>	<i>Catopithecus</i>	Adapoid
Upper and lower P2	Present	Absent	Present
Incisors spatulate	No	Yes	Yes
Sexual dimorphism	No	Yes	Yes
Prominent central incisor jugum	Yes	No	No
Inter canine distance narrow, pinched	Yes	No	No
Postorbital closure	Partial	Complete	None
Zygomatic-alisphenoid contact	Yes	Yes	No
Lacrimal foramen inside orbit	No	Yes	Variable
Maxillary tuber with septal flange	Yes	No	No
Zygomaticofacial foramen	Absent	Moderate	Large
Interorbital region and nasal bones	Narrow	Broad	Broad
Olfactory bulb	Small	Moderate	Large
Sagittal crest	No	Yes	Yes
Ascending process of premaxilla	Narrow	Broad	Broad
Mandibular symphysis fused	No	No	Variable
Face deep	No	Yes	Yes
Position of pyramidal process of palatine and pterygoid processes	Medial	Lateral	Lateral
Shape of pyramidal process of palatine	Delicate	Robust	Robust
Posterior palatine torus	Present	Absent	Absent
Ectotympanic tubular in shape	Yes	No	No
Ectotympanic ventrally attached	Yes	Yes	No
Suprameatal foramen	Yes	No	No
Position of postglenoid foramen relative to glenoid fossa	Medial	Behind	Behind
Parotic fissure	Present	Absent	Absent
Foramen magnum position	Forward	Medium	Back
Jugular foramen	Small	Large	Medium
Shape of the temporomandibular articular surface	Guttered	Flat	Flat
Occipital condyle articular surface posteriorly convex downward	No	Yes	Yes
Basilar part of occipital bone	Narrow	Broad	Broad
Large promontory canal	Yes	Yes	Variable

¹ Dental occlusal features are not listed; these support a close relationship between adapoids and oligopithecines (Rasmussen and Simons, 1988). Adapoid cranial structure derived from the following publications: Franzen (1987, 1994); Gazin (1958); Gingerich (1981a); Gingerich and Martin (1981); Gregory (1920); Gunnell (1995); Lanèque (1993); Rasmussen (1990); Stehlin (1912); Thalmann et al. (1989).

could argue that the single most influential idea in primate evolutionary studies for a century has been the notion that tarsiers and anthropoideans are somehow specially related to each other (Hubrecht, 1896). For this reason alone, we would be remiss not to make a specific comparison between *Catopithecus* and *Tarsius* (Table 8). In our view, the earliest known anthropoidean cranium is of central importance in addressing the question of whether anthropoideans are descended from a tarsioid primate. The fossil evidence suggests that derivation of *Catopithecus* and *Tarsius* from a common source removed from known Eocene primate radiations is not a parsimonious hypothesis. It requires a large number of substantial evolutionary changes (Table 8).

Omomyids are an early Tertiary radiation specifically related to extant *Tarsius* (Wort-

man, 1903; Teilhard de Chardin, 1921; Clark, 1959; Simons and Russell, 1960; Simons, 1961; Gingerich, 1981b; Rosenberger, 1985; Beard et al., 1991; Beard and MacPhee, 1994; Rasmussen, 1994). Quite apart from the morphological evidence that argues against homology of the tarsier and anthropoidean postorbital plates (Simons and Russell, 1960; Tattersall, 1973; Cachel, 1979b; Simons and Rasmussen, 1989; Beard and MacPhee, 1994), the absence of postorbital flanges in omomyids provides strong support for the hypothesis that the condition in *Tarsius* evolved in parallel to that of Anthropoidea (for an opposing viewpoint, see Cartmill, 1980, 1994; Ross, 1994).

Adapoids

Paleontological work continues to reveal previously unknown diversity within the ad-

TABLE 9. Classification of *Catopithecus browni*

Order Primates Linnaeus, 1758
Suborder Neopithecini Wortman, 1903
Hyporder Anthropeidea Mivart, 1864
Infraorder Catarrhini E. Geoffroy, 1812
Superfamily Propitopithecoidea Straus, 1961
Family Propitopithecidae Straus, 1961
Subfamily Oligopithecinae Simons, 1989
Genus <i>Catopithecus</i> Simons, 1989
<i>Catopithecus browni</i> Simons, 1989

apoid primates. The subgroup of adapoids usually examined as possible ancestors of Anthropoidea are now classified as the subfamily Cercamoniinae in the family Notharcidae (Franzen, 1994). It is probable that the cercamoniines deserve family rank but this is a hypothesis we are not prepared to enlarge on at the present time. Among the putative new adapoids are several forms described as cercamoniines from the Eocene of North Africa (*Djebelemur*, Hartenberger and Marandat, 1992; *Omanodon* and *Shizaradon*, Gheerbrant et al., 1993; *Aframoni*, Simons et al., 1995).

Adapoids are probably related to the basal radiation of Anthropoidea, as first suggested on the basis of the carotid circulation and the relationships of the lacrimal bone (Wortman, 1903), and later supported primarily by the morphology of the anterior dentition (Gingerich and Schoeninger, 1977; Gingerich, 1981a; Rasmussen, 1986; Franzen, 1994), sexual dimorphism in canine size (Gingerich, 1981a; Simons et al., 1995), the structure of the cheek teeth (Rasmussen and Simons, 1988), and the annular, rather than tubular, ectotympanic (Gingerich, 1973; Rasmussen, 1990). Other features that are possibly shared features of an adapoid-anthropoidean clade are more difficult to evaluate because of the smaller sample of known relevant elements (e.g., articular relationships of the centrale; Beard et al., 1988; Beard and Godinot, 1988; Godinot and Beard, 1991; Godinot, 1992; Franzen, 1988, 1994). To reflect the phylogenetic link between adapoids and Anthropoidea, we resurrect Wortman's (1903) taxon Neopithecini, at a new rank (Table 9). It is noteworthy that Wortman's informed and cohesive classification preceded the better known classifications of Gregory (1915) and Pocock (1918). We consider this nomenclatorial action a

conservative alternative to erecting a new taxon.

Catopithecus reveals that some features formerly considered to be possible shared-derived features of an adapoid-anthropoidean clade have evolved in parallel in the two groups (e.g., large body size; fused mandibular symphysis). The occurrence of small size and unfused symphysis in an early catarrhine indicates that larger size and fused symphysis was not a feature of the ancestral anthropoidean, but rather one that evolved in parallel in the New and Old World forms.

The anterior dentition of *Catopithecus* is one line of evidence that strongly supports a phyletic link between adapoids and anthropoideans. The spatulate incisors shared by adapoids and anthropoideans are often dismissed as primitive, therefore implying that they provide no support for special relationship between the two groups (Rasmussen et al., 1995). However, there is no real evidence for such an interpretation. The anterior dentitions of adapoids and anthropoideans closely resemble each other but differ substantially from all other primate groups (omomyids, tarsiids, strepsirrhines) and other potential primate outgroups (Plesiadapiformes, Dermoptera, Scandentia, various insectivoran groups). The shared assemblage of features includes the following: incisors are implanted relatively vertically; the lower laterals are larger than the lower centrals (also found in *Washakius*); the upper and lower central incisor crowns are spatulate, with broad and relatively flat occlusal edge; the mesial occlusal edge of the upper central incisors converge at the midline to meet near their apex, but they have a moderate midline interincisal diastema at the alveolar level leaving an apically closed, triangular gap between the upper incisors; the upper and lower lateral incisor crowns are ovoid in outline; the canines are relatively large, cylindrical teeth; the upper canine in some adapoids and anthropoideans has a mesial groove; the canines are sexually dimorphic in size. No other mammal, primate or otherwise, matches the assemblage of features seen in the anterior dentition of adapoids and anthropoids. The adapoid-anthropoidean pattern cannot be dismissed as primitive, and the detail of the similarity

argues against homoplasy. There appears to have been evolutionary continuity in the form of the spatulate incisors and large canines spanning the taxonomic groups that include adapoids, parapithecids (such as *Apidum*), basal anthropoids of uncertain family status (like *Arsinoea*), and primitive catarrhines (such as *Catopithecus*). Detailed evaluation of the individual characters of importance to the adapoid-anthropoidean hypothesis are presented in numerous other publications, viz.: Wortman (1903); Gingerich (1975); Gingerich and Schoeninger (1977); Greenfield (1983); Rasmussen (1986, 1990, 1994); Franzen (1987, 1994); Rasmussen and Simons (1988); Rasmussen et al. (1995); and Simons (1995a,b).

CONCLUSIONS

Anthropoidean divergence

The skull of *C. browni* is morphologically very primitive for a primate lying near the base of the catarrhine radiation. Among the most notable primitive features are the following: unfused mandibular symphysis; small brain size; relatively large olfactory bulbs; relatively large dentition compared to the face and braincase; complete trigonid on the first lower molar. At the same time, *Catopithecus* shows derived anthropoidean and catarrhine traits, the most notable of these being the platyrrhine-like extent of post-orbital closure, an anthropoidean-like auditory region, and the reduction of the dental formula to two premolars per quadrant. The assemblage of traits observed in *Catopithecus* indicates that the original divergence among catarrhines, platyrrhines, and parapithecoids occurred at a primitive stage; many of the traits shared by the three major anthropoidean radiations have been obtained convergently. The recognition that the parapithecoids retained many prosimian-like and primitive anthropoidean features (Fleagle and Kay, 1987) led to the conclusion that parapithecoids may have diverged from the combined catarrhine-platyrrhine clade before the latter two split from each other. However, now it is known that the catarrhine clade was also surprisingly primitive. This observation re-opens the question of the branching sequence of

the parapithecoids, catarrhines, and platyrrhines; if all three groups were basally very primitive, there is no compelling reason to believe that parapithecoids diverged first. If Paleogene platyrrhines are ever found, we predict that they, also, will retain a higher proportion of primitive features than would have been predicted by morphotype reconstructions relying upon the distribution of common features among extant anthropoideans.

Adaptations of *Catopithecus*

In body size, *Catopithecus* was very small, resembling the callitrichids among extant anthropoideans. Previously, a body weight range was estimated (Rasmussen and Simons, 1992) using several regression equations derived from dental samples of modern anthropoideans, all primates, or prosimians (Gingerich et al., 1982; Conroy, 1987). The weight range estimated for *C. browni* after considering several factors was 600–900 g (Rasmussen and Simons, 1992). Now that the cranium of *Catopithecus* is known, it is clear that it has a prosimian-like relationship between the size of the dentition and that of the cranium (relatively large teeth, small cranium). Therefore, using regressions derived solely from anthropoidean species will overestimate the body weight of *Catopithecus*. Using the prosimian regression of Conroy (1987), the resulting point estimate without confidence intervals for *C. browni* is 472 g, suggesting that the estimates of Rasmussen and Simons (1992) should be reduced. Taking sexual dimorphism and individual variation into account, we now suggest a new, lower weight range of 400–800 g. Postcranial bones tentatively assigned to *Catopithecus* are similar in size to those of *Saimiri* and *Callicebus* (Gebo et al., 1994), but the appropriate elements are not available to allow use of published regressions for predicting body weight from postcrania.

The morphology of the dentition and masticatory system of *Catopithecus* are more similar to those of *Saimiri* than of any other extant primate. The shape and biomechanical properties of the mandible of *Catopithecus* match closely those of *Saimiri*, except for the fused symphysis and extra premolar

of *Saimiri* (compare Fig. 12 with Hershkovitz, 1977:190). The upper molars of the two genera resemble each other in their subquadrate shape with a slight, cristiform hypocone. The occurrence of canine dimorphism in the two genera is also a shared similarity which is absent from callitrichids. If the dental and mandibular similarities reflect shared elements of the diet, *C. browni* can be interpreted as a fruit and insect eater like *Saimiri* (Mittermeier and Van Roosmalen, 1981; Terborgh, 1983). This conclusion is consistent with a more detailed examination of molar occlusal features as they relate to diet (Rasmussen and Simons, 1992).

The sample of orbit size for *C. browni* confirms that this species was diurnal. The large olfactory bulb and broad interorbital breadth are interpreted as adaptations for well-developed olfactory abilities, perhaps used in social communication, similar to that of extant callitrichids. The sexually dimorphic canines indicate a polygynous social structure, resembling *Saimiri* and small extant catarrhines, such as *Miopithecus* (Fleagle et al., 1982; Kay et al., 1988). The small body size, the relatively small brain, and the dental eruption sequence may allow us to make a tentative suggestion about life history pattern. If the eruption sequence shared by *Catopithecus* and small platyrrhines reflects shared developmental trajectories (Smith, 1989; Smith et al., 1994), then we hypothesize that offspring of *Catopithecus* developed quickly by catarrhine standards, perhaps being dependent on their mothers for less than 1 year and becoming sexually mature by no later than 2 years.

Phylogeny of *Catopithecus*. It is clear that, as in most pivotal fossil primates, the phylogeny of *Catopithecus* will engender much discussion, both as this genus relates to later anthropoideans and to earlier Eocene groups. Figure 14 illustrates our phylogenetic conclusions based on the morphological characters that we hypothesize reflect the actual branching sequence.

In particular, we conclude that the genus does belong in the catarrhine clade (as defined by its divergence from platyrrhines, not by the common ancestor of only those catarrhines that happen to survive to the

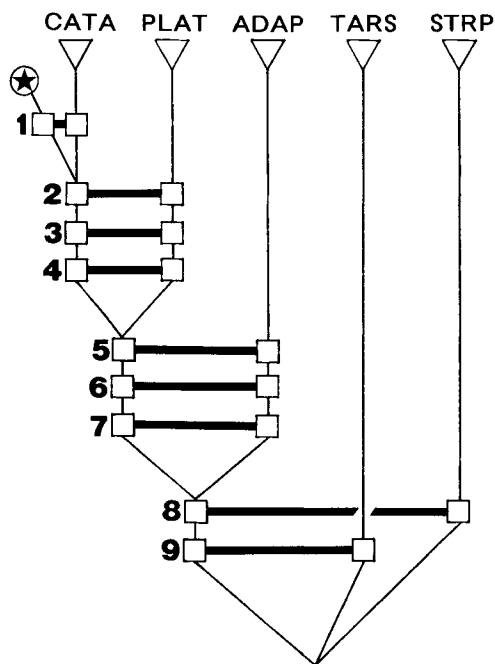


Fig. 14. Phylogeny of *Catopithecus browni* (star) showing clades defined by nine specialized traits: 1, loss of second premolars; 2, postorbital closure; 3, annular ectotympanic ventrally fused to bulla wall (independently derived in some strepsirhines); 4, fused metopic suture in adults (distributed occasionally among other primates); 5, spatulate incisors; 6, sexual dimorphism in canine size; 7, upper canine with mesial groove, and distal honing relationship with lower premolar; 8, loss of parotic fissure (Beard and MacPhee, 1994; Ross, 1994); 9, large promontory canal (variable among adapoids; Gunnell, 1995). ADAP, Adapoidea; CATA, Catarrhini; PLAT, Platyrrhini; STRP, Strepsirhini, used in the strict sense of including only Malagasy taxa and Lorisidae; TARS, Tarsiiformes. Besides the anterior dental features listed, Neopithecini (CATA + PLAT + ADAP) is also supported as the most parsimonious grouping among the known Eocene primates based on a broad sample of cranial traits (Table 8). The divergence among Neopithecini, Tarsiiformes, and Strepsirhini is considered to be an unresolved three-way split, probably dating back to the Paleocene.

present). The most important derived feature indicating catarrhine affinity is the loss of second premolars. Also, the morphological and stratigraphic relationships between *Catopithecus*, *Oligopithecus*, and *Proplioptithecus* are very compelling to us (Table 6).

As for how *Catopithecus* relates to non-anthropoidean Eocene forms, we conclude that *Catopithecus* belongs in Neopithecini

along with cercamoniine adapoids, and possibly other adapoids as well. The cranial morphology of *Catopithecus* argues strongly against a special affinity between anthropoideans and tarsiiform primates (Table 8). In our judgment, Anthropeidea can only be derived from adapoids or from an unknown group; if an unknown African group does exist, it will probably be related to adapoids.

Our preferred classification of *Catopithecus* is presented in Table 9.

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